HEREDITY AND EVOLUTION IN PLANTS

GAGER

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FRONTISPIECE

Restoration of a scene along a sluggish creek in Texas and New Mexico during the late Carboniferous (Upper Pennsylvanian) and early Permian times. The lowlands of this period doubtless swarmed with reptiles such as shown in the picture, and with other animals, now extinct. Some specimens of the giant "dragon-flies" had a spread of wings of two feet. The fern-like trees and the bushy plants in the foreground are Cycadofilicales. To the right of the water are wide stretches of the huge scouring rush (*Calamites*); on the left bank of the stream are the unbranched *Sigillarias* (still as prominent as earlier in the coal period), and on higher ground to the left the branched *Lepidodendrons*. One must view this scene as one of many such landscapes, with ever-varying detail, along streams and inlets. *Cordaites*, which in later Devonian time made the first great forests of which there is record, is still present, though not shown. So, too, there are hidden in the recesses of the forest the forerunners of the modern coniferous types, as well as other forms destined to give rise to the angiosperms. (Landscape from Williston, adapted from Neumayr.)

Frontispiece.

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HEREDITY
AND
EVOLUTION IN PLANTS

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BY

C. STUART GAGER

DIRECTOR OF THE BROOKLYN BOTANIC GARDEN

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To the Memory of

BENJAMIN STUART GAGER

"What a science Natural History will be when . . . all the laws of change are thought one of the most important parts of Natural History."—
Charles Darwin. (*Letter to J. D. Hooker.*)

PREFACE

The present little book was originally intended to be merely a reprint of Chapters XXXI to XXXVIII of the author's *Fundamentals of Botany*. The reprinting of those chapters was suggested by comments received from various correspondents, who pointed out that the subject matter which they cover had not been elsewhere presented in so concise a treatment in one volume, and in a manner suited, not only to beginning students, but also to more general readers. The chapter on Experimental Evolution has received the approval of the author of the mutation theory, as being an accurate presentation of the essentials of that theory. "I have especially appreciated," writes Professor de Vries, "the statement of the difference between fluctuating and saltative variation, which is, to my mind, the real empirical basis for the theory, far more than the experiments on mutation with single plants. The relation of my view to Darwinism is misunderstood by many authors, and it is a great satisfaction to me that you have outlined it in such a plain way."

In the preparation of the copy for reprinting, considerable new matter has been added, certain sentences and paragraphs, pertinent only to an elementary text-book, have been omitted, and others recast, and several fresh illustrations have been introduced, either as new or as substitutes.

Chapters X, Geographical Distribution, and XIII, The Great Groups of Plants, and the Bibliography are new. No attempt has been made to cite the voluminous periodical literature in the Bibliography, but needless to state, this has been freely consulted and drawn upon. Numerous citations are given as foot-notes, especially in Chapter X.

In going over the chapters it also became evident that since, in order to read them understandingly, one must have a clear conception of the facts of the lift history of a vascular plant, it would be best to introduce from the *Fundamentals of Botany* the three chapters (viz. XII–XIV) on the life history of the fern. As stated in the *Preface* to that book, while the ultimate problem of botany is the development of the kingdom of plants, the more immediate and fundamental problem is the development of the individual plant. "Ontogeny is fundamental because without a knowledge of its processes the processes of phylogeny cannot be comprehended. Phylogeny is the ultimate problem because its complete solution involves an orderly description of all the phenomena of plant life, and their relation to each other."

The author is specially indebted to Dr. O. E. White, curator of plant breeding in the Brooklyn Botanic Garden, for a careful reading of the entire manuscript and for many valuable suggestions; also to Mr. Norman Taylor, curator of plants, in connection with Chapter X, and to Dr. Alfred Gundersen, associate curator of plants in the same institution, for numerous constructive criticisms in connection with Chapter XIII. The diagram showing the apparent affinities and approximate geological distribution of the main groups of vascular plants (p.

248) originated with Dr. Gundersen, but has been modified, as here printed, in certain details for which the author alone is responsible. Grateful acknowledgment is made to Dr. Ralph E. Cleland for photo prints of Figs. 74 and 75 from negatives made by him on the summit of Mt. Madison (Adirondacks); and to Prof. Harvey W. Shimer, author, and The Macmillan Co., publisher, for permission to reproduce Fig. 66.

If the following pages shall prove to be a source of reliable and readable elementary information to those interested in the subjects treated, the object of the book will be accomplished.

Brooklyn Botanic Garden,
March 25, 1920.

C. Stuart Gager.

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HEREDITY AND EVOLUTION IN PLANTS

CHAPTER I

LIFE HISTORY OF A FERN

1. Life History.—Every plant, in the course of its existence, passes through a series of changes in orderly

FIG. 1.—A fern (*Anisosorus hirsutus*), showing portion of the stem above ground.

sequence. Like an animal, every plant begins life as a single cell, the *egg*, or the equivalent of an egg. Except in some of the lower forms, the egg develops into an

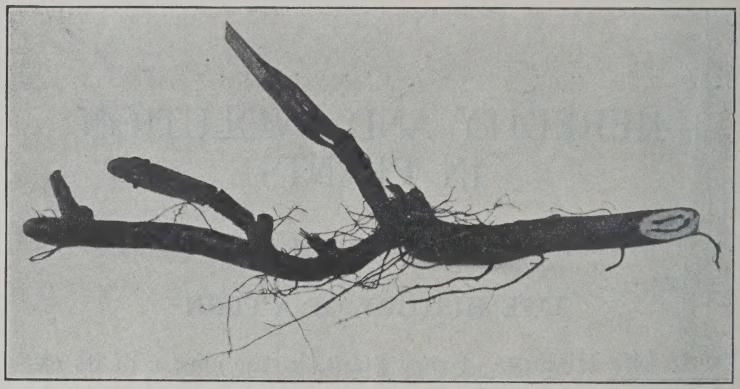


FIG. 2.—Portion of the rhizome of the common brake (*Pteris aquilina*) showing a cross-section view at the right.

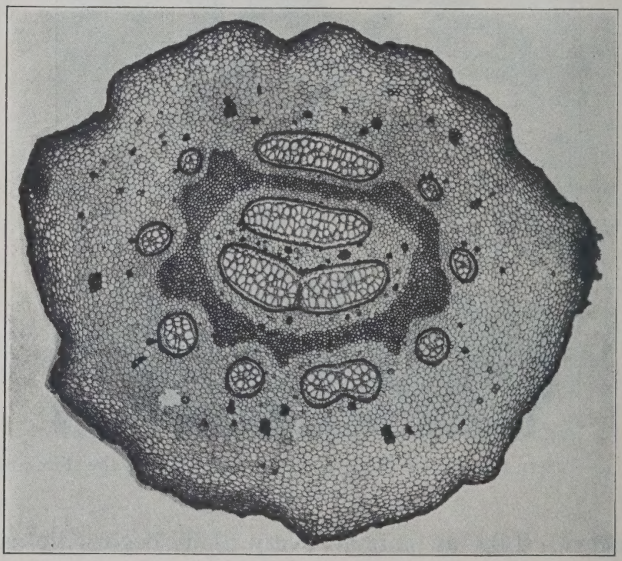


FIG. 3.—Cross-section of the rhizome of the bracken fern (*Pteris aquilina*), showing the tissue systems. Greatly magnified.

embryo, and the embryo matures into an *adult*. By a series of more or less complicated processes the adult eventually gives rise to another egg, like the one from which it came, thus completing one life-cycle and initiating another. These various changes constitute the *life*

FIG. 4.—Tree ferns on the military road between Cayey and Caguas, Porto Rico. (Photo by M. A. Howe.)

history of the individual. The various stages of life history common to most plants are nowhere more clearly illustrated than in the ferns.

2. Description of a Fern Plant.—The more common ferns of temperate regions have underground stems or *rhizomes* (sometimes called *root-stocks*), so that only the

leaves appear above ground.[1] The stem may be branched or unbranched. When branched, the branches are produced without reference to the insertion of the leaves, in contrast to the habit of higher plants of forming branches only in the upper angle (*axil*) between the stem and leaf-stalk. There is always a terminal bud at the

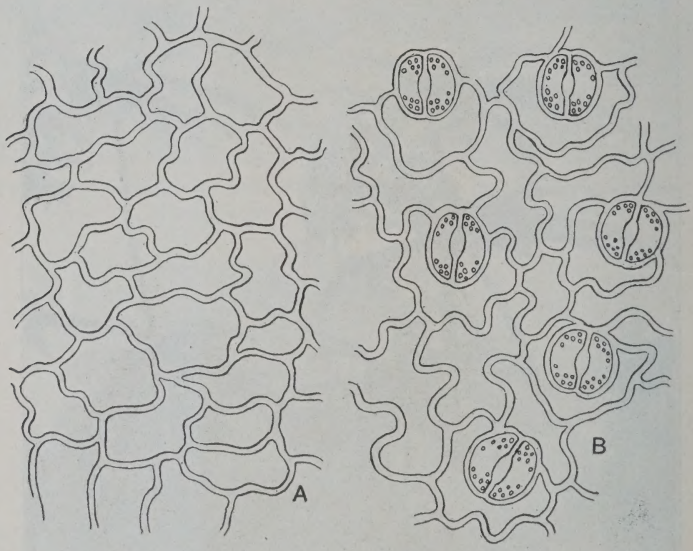


FIG. 5.—*A*, Upper epidermis; *B*, lower epidermis of the leaf of the fern, *Drynaria meyeniana*. (Camera lucida drawing.)

tip of the fern-stem (and of the branches when any occur); and the leaves are usually attached just back of this tip. The stems are commonly (though not always) covered by hairs or scales (Fig. 1), and on their older portions, at some distance back from the tip, may be seen the *scars*, or the ends of leaf-stalks, left by old leaves that

[1] The leaves of ferns are often called *fronds*.

have died and fallen away. The rhizome bears true roots (Fig. 2), and its tissues are differentiated into epidermal, fundamental, mechanical, and conducting systems (Fig. 3). In tropical countries there are "tree ferns,"

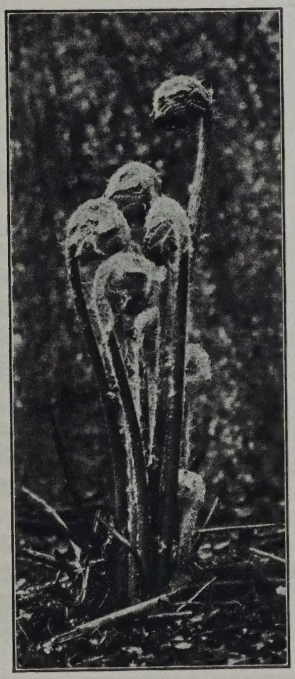


FIG. 6.—*Osmunda Claytoniana*. Young sporophylls, showing circinate vernation. Note the spore-bearing pinnæ.

with upright stems, and this type of fern is common among the fossil plants of earlier geological ages (Fig. 4). There are also climbing ferns.

3. Two Kinds of Fern-leaves.—Careful examination of the leaves of certain mature ferns will disclose the fact

that they are not all alike. Some of them are merely *foliage-leaves*, and do not differ in any essential point from the foliage-leaves of higher plants, such as the maple or lily; they possess stomata for the exchange of gases and

FIG. 7.—Portions of the sporophylls of two ferns to show the sori. On the left *Polypodium punctatum* (L.) Sw.; on the right a variety of *Pteris longifolia*, with sporangia marginal on the pinnules.

water-vapor with the outer air (Fig. 5), and they also resemble the leaves of higher plants in their internal structure. All fern-leaves, however, have a very characteristic arrangement in the embryonic or bud condition, being

coiled up from the tip. As the leaves grow they unroll, and in some ferns, at certain stages, they often closely resemble the neck of a violin (Fig. 6). The leaf-blade

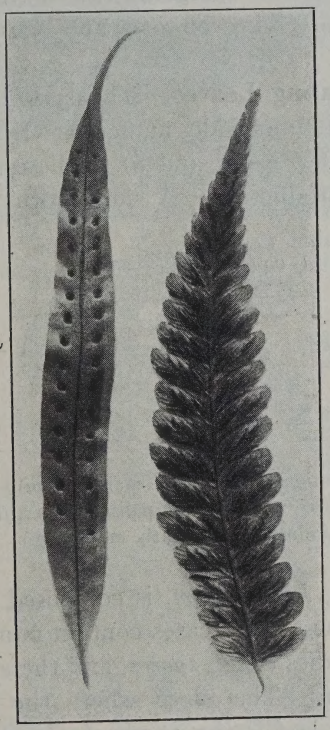


FIG. 8.—Sporophylls of two ferns. At the left, a species of *Polypodium* (*Phymatodes*), having no indusium; at the right, *Diplazium zelanicum*.

possesses veins of fibro-vascular bundles that pass down the leaf-stalk and through the stem to the roots. Because of the possession of these vascular bundles, ferns (and all other plants of which this is true) are called *vas-*

cular plants. These leaves perform all the functions performed by the foliage-leaves of other plants, the most important of which are the manufacture of organic, carbohydrate food from inorganic raw materials (*photosynthesis*), and the giving off of water vapor from within (*transpiration*).

4. Spore-bearing Leaves.—The second type of fern-leaf bears, on its underside, numerous "fruit-dots" or *sori* (singular *sorus*) (Figs. 7 and 8). These structures have to do with reproduction. A single sorus of such a fern

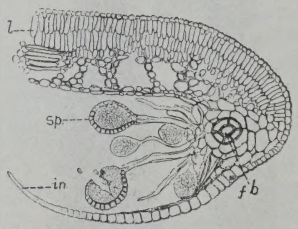


FIG. 9.—Cross-section through the marginal sorus of a sporophyll of the bracken fern (*Pteris aquilina*). *l*, palisade layer; *fb*, vascular bundle; *sp*, sporangium; *in*, indusium. (Greatly magnified.)

as, for example, *Polypodium*, is composed of a cluster of tiny stalked cases. The cases contain minute unicellular reproductive bodies called *spores*, and the entire structure is a *sporangium*. The place where the sporangia are attached to the leaf is the *sporangiophore*[1] (Fig. 9), and over all is often found a thin membranous covering, the *indusium* (Figs. 9 and 10). In some ferns the indusium is lacking, and the sorus is naked. Spore-bearing leaves are called *sporophylls*, and plants that bear sporophylls are called *sporophytes*.

[1] Also called *receptacle*.

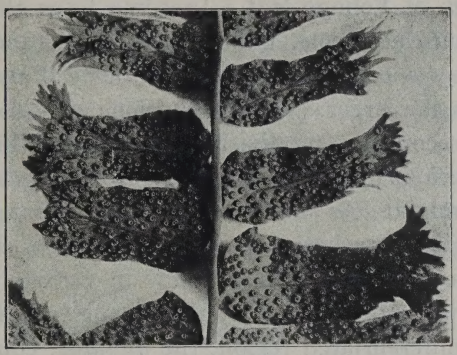


FIG. 10.—*Cyrtomium falcatum.* Under (dorsal) surface of a portion of a sporophyll, showing the numerous sori on the pinnæ.

FIG. 11.—Fern leaves, showing various degrees of subdivision or branching of the blade. *A, Phyllitis; B, Polypodium; C, Pteris; D, Adiantum.*

5. Types of Foliage-leaf.—In some ferns the foliage-leaf presents a simple, unbranched blade, and petiole; but in other species the blade is variously branched. In such cases the larger, primary divisions are called *pinnæ*, and the secondary subdivisions *pinnules*. Illustrations of these various types are shown in Fig. 11.

6. Sporangia.—As noted above, each sporangium consists of a spore-case borne on a stalk (Fig. 12). The structure of the case varies considerably in various groups of ferns, but it usually possesses walls only one cell thick, with a clearly differentiated region, the *annulus*, composed of cells whose radial and inner cell-walls are greatly thickened. Various types of spore-cases are illustrated in

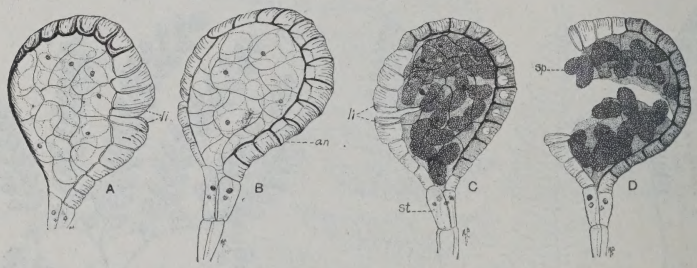


FIG. 12.—Sporangia of an undetermined species of fern; *li*, lip-cells; *an*, annulus; *st*, stalk; *sp*, mature spores. Each of the four nuclei in the upper cells of the stalk is in the terminal cell of one of the four vertical rows of cells that compose the stalk.

Fig. 13. Among the group of ferns which are now most common, and to which the bracken fern (or "brake"), the maiden-hair fern, the common polypody, and others belong, the sporangium always originates from a single epidermal cell. Ferns whose sporangia thus originate are called *leptosporangiate* ferns (*Cf.* p. 29). The walls of their spore-cases are always only one cell thick, and

always possess some form of annulus. As the sporangia mature the spore-case itself becomes differentiated into two distinct kinds of tissue, namely, *vegetative tissue* on the outside, forming the wall and *reproductive tissue* within, from which the spores are developed.

7. Number of Spores.—The number of spores produced by a vigorous fern is a great revelation to one who has never given such matters careful thought. Pro-

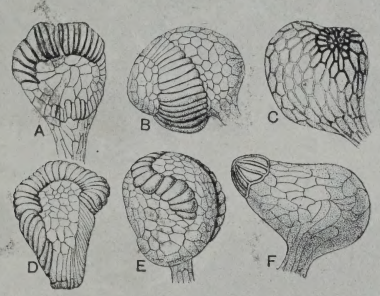


FIG. 13.—Types of fern sporangia. *A, Loxsoma Cunninghami; B, Gleichenia circinata; C, Todea barbara; D, Thyrsopteris elegans; E, Matonia pectinata; F, Lygodium japonicum.* (Redrawn from various sources.)

fessor Bower, of Glasgow, has called attention to this fact in the following words:

"A rough estimate may be made of the numerical output of spores from a large plant of the Shield fern, as follows: In each sporangium 48[1] spores may be formed; a sorus will consist of fully 100 sporangia, usually more; 20 is a moderate estimate of the sori on an average pinna; there may be fully 50 fertile pinnæ on one well-developed leaf, and a strong plant would bear 10 fertile leaves. $48 \times 100 \times 20 \times 50 \times 10 = 48{,}000{,}000$. The output of spores on a strong plant in the single season will thus, on a moderate estimate, approach the enormous number of fifty millions."

8. Types of Sporophylls.—In many ferns the leaves serve both vegetative and reproductive functions in about

[1] Bower gives this number as the characteristic output for the species *Aspidium Filix-mas*. In other species the number may be 64.

equal degree, as in the case of *Polypodium* mentioned above. In some species, however, there are two kinds of leaves—one devoted entirely to vegetative functions, and another to the reproductive, or spore-producing function (Fig. 14); between these two extremes all grades of transition are found (Fig. 15). But however widely the sporo-

FIG. 14.—The cinnamon fern (*Osmunda cinnamomea*), showing foliage leaves and sporophylls.

phyll departs from a foliage-leaf in appearance, it must, nevertheless, be regarded as morphologically a leaf. As partial evidence of the true foliar nature of sporophylls, there may be cited the interesting experiment of Atkinson, who, by removing the true foliage-leaves just beginning to unfold in the spring, was able to induce developing sporophylls to alter their character, and become transformed

FIG. 15.—Clayton's fern (*Osmunda Claytoniana*), showing sporophylls in the center, surrounded by foliage leaves.

into foliage-leaves. Similar results were also obtained by Goebel. These experiments indicate that foliage-leaves and sporophylls are very closely related to each other,

FIG. 16.—Portion of a leaf of a fern (*Tectoria cicutaria*) that bears bulbils on both the upper and lower surfaces of its leaves. Plantlets develop from the bulbils while they are still attached.

and demonstrate clearly that foliage-leaves may be produced by the *sterilization* of spore-bearing leaves. The interesting question here naturally arises as to whether, in the evolutionary development of the plant kingdom

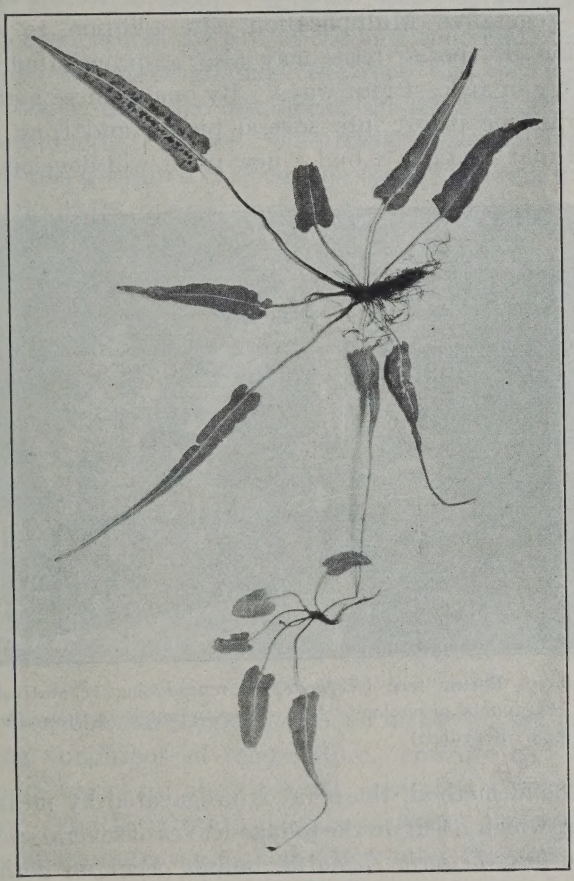


FIG. 17.—Walking fern (*Camptosorus rhizophyllus*). The smaller, lower plant originated at the tip of a leaf of the larger plant, and one of its leaves has, in turn, struck root.

through long geological ages, foliage-leaves have in general originated by the sterilization of spore-bearing organs.

9. Vegetative Multiplication.—In addition to reproduction by spores, ferns may also be propagated vegetatively in at least four ways. By one of these methods, the rhizome is cut into several pieces, and from every piece that contains a bud a new plant will develop. By

FIG. 18.—A Boston fern (*Nephrolepis*), reproducing vegetatively by means of runners or stolons. The parent plant is in the round pot. (After R. C. Benedict.)

the second method, the plant is progagated by means of *bulbils*, which occur on the foliage-leaves of several species. In the fern *Tectoria cicutaria*, bulbils occur on both the upper and under sides of the leaf (Fig. 16). These bulbils fall to the ground, and under suitable conditions of light, moisture, and temperature give rise to new fern-plants. One of the ferns native to the eastern United States (*Cystopteris bulbifera*) received its specific name from the

fact that it bears bulbils. A third method is illustrated in the very interesting "walking fern" (*Camptosorus rhizophyllus*), where the tips of the long acuminate leaves rest upon the moist ground, take root, and develop an entire new plant at the distance of the leaf's length from the parent fern (Fig. 17). The result of several repetitions of this suggested the common name "walking fern." A fourth method is by means of *stolons* or "runners" (Fig. 18).

10. Dispersal of Spores.—After the spores are mature the essential need is that they become dispersed, so that they may find favorable conditions of moisture, temperature, light, and soil for development; for, with rare exceptions, such conditions do not obtain within the spore-case. Moreover, if the spores remained within the sporangia they would be so greatly crowded that only a very small percentage of them would be able to develop into new plants. When the spores are ripe the spore-case opens, and by various movements the spores are expelled, often to a considerable distance; by wind and other agencies they may be carried still further from the parent plant.

11. Germination of Spores.—After dispersal, and under favoring conditions of temperature, moisture and light the spore begins to absorb water, and soon commences to grow. As the internal pressure increases, the walls of the spore are burst apart, and a tiny tube, the *germ-tube* or *protonema* (first thread), begins to develop. This process is *germination*. Shortly, near the wall of the spore, a smaller, slender tube develops as a branch of the germ-tube (Fig. 19). This is the first of innumerable root-like bodies, or *rhizoids*, which will help to hold the new plant

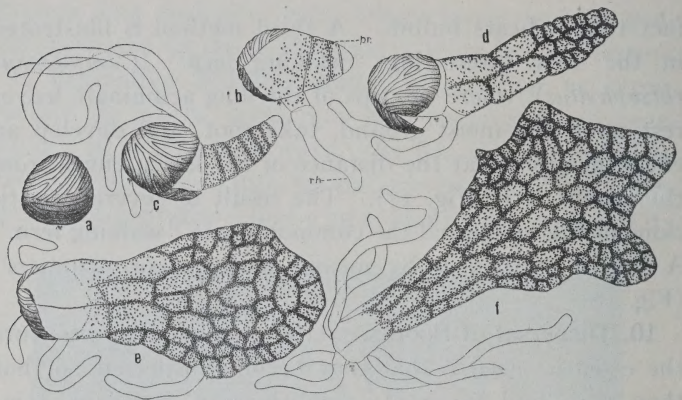


FIG. 19.—Germination of the spores of a fern. *a*, Before germination; *b*, early stage, showing protonema (pr.), and first rhizoid (*rh*); *c*, *d*, *e*, *f*, successive stages in the development of the prothallus.

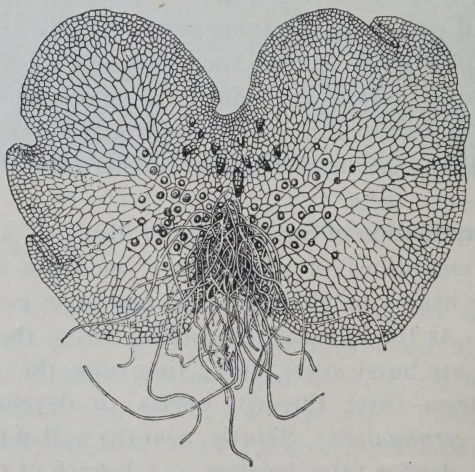


FIG. 20.—Prothallus of a fern. Archegonia on the (central) cushion, near the notch; antheridia among the rhizoids, below. (After Margaret C. Ferguson.)

firmly to the soil, and also serve to take in water and dissolved mineral nutrients.

12. The Prothallus.—Before the germ-tube has greatly enlarged, it becomes divided into two cells, and then, by successive cell-divisions, into an increasing number. Meanwhile chlorophyll bodies begin to appear, but never in the rhizoids. The final product of these cell-divisions and growth is a tiny, flat, green body, often (but not always) heart-shaped, with a central portion, the *cushion*, several cells thick, and a marginal part, the *wings*, of only one cell in thickness. Because of its flatness this little plant (for such it is) is called a *thallus*; and because it precedes, in the order of reproduction, the new sporophyte, it is called the *prothallus* (Fig. 20). It is usually possible to divide the prothallus into right and left halves, similar in shape and in other characters, and hence it is said to possess *bilateral symmetry*.

CHAPTER II

LIFE HISTORY OF A FERN (Concluded)

The prothallus, as just described, bears little resemblance, indeed, to the fern plant with which we are commonly familiar. In fact, the relation between the two was not understood, nor even suspected, until about 1848, when Count Lesczyc-Suminski, a Polish botanist, first gave a connected description of the life history of the fern. We shall now proceed to follow the steps which lead from the prothallus to the new sporophyte.

13. Dorso-ventral Differentiation.—The appearance of the first root-like body, or rhizoid, was noted above. As the prothallus develops the rhizoids become more and more numerous, forming a mass of fine thread-like bodies on the under side, opposite the notch, of the heart-shaped prothallus. The presence of rhizoids, and of other structures soon to be described, makes it easy to distinguish at once the surface that bears them from the opposite surface. Since the surface bearing the rhizoids lies normally next to the substratum it was called the *ventral* surface, while the opposite surface was called *dorsal*. As now used, the terms dorsal and ventral are morphological terms, and have no reference to the manner in which the prothallus lies. Normally the ventral surface is the under one and the dorsal surface the upper, but the application of the terms would not be changed if the differentiated prothallus should happen, by any chance, to lie upside

down. The dorsal surface would then be the under surface, and the ventral surface the upper one. Organisms or organs having two such surfaces clearly distinguishable are said to have *dorso-ventral differentiation*. Among many other structures thus differentiated are foliage-leaves, sporophylls, man, fishes, and other animals. In buds the dorsal surface of leaves is the upper or outer surface; when foliage leaves are fully expanded the dorsal surface is commonly underneath, and the ventral surface above.

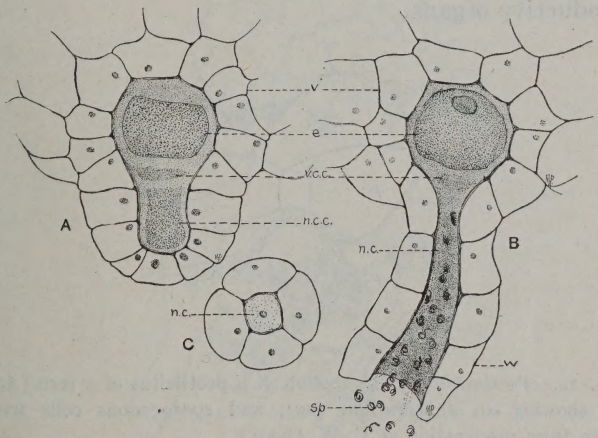


FIG. 21.—Archegonia of a fern (*Adiantum*). *A*, young archegonium; *B*, mature; *C*, top view, showing terminal cells of the four rows of wall cells; *v*, wall of venter; *e*, egg; *v.c.c*, ventral canal-cell; *n.c*, neck-canal; *sp*, sperms entering the neck-canal. *A* and *B* in longitudinal section.

14. Reproductive Organs: Archegonia.—Examination of the ventral surface of a mature prothallus with a lens will reveal near the notch and on the cushion, several tiny flask-shaped bodies, the *archegonia*. Each archegonium consists of a wall, one cell thick, and contents (Fig. 21). The *neck* projects away from the surface

and is usually slightly curved, while the remainder, the *venter*, is imbedded in the tissue of the cushion. As the archegonium approaches maturity it is seen to contain three cells; a long *neck-canal cell*, nearly filling the neck, an *egg-cell* or *ovum*, filling the venter, and between these two a *ventral-canal cell*. The egg is the female reproductive cell. As it matures, the other two cells become disintegrated into a mucilaginous mass that fills the neck-canal. Since the archegonia contain the eggs they are the female reproductive organs.

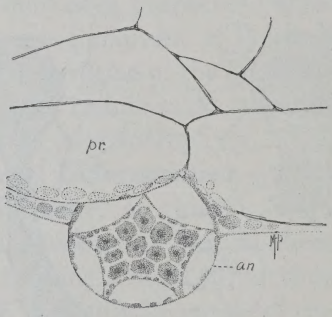


FIG. 22.—Portion of a cross-section of a prothallus of a fern (*Adiantum*), showing an antheridium (*an*), and sporogenous cells within. (Drawn from preparation of E. W. Olive.)

15. Reproductive Organs: Antheridia.—Search among the rhizoids will reveal another class of organs, the *antheridia*, globular and also having walls only one cell thick. These are the male reproductive organs. At maturity they contain a large number of tiny motile cells, composed chiefly of a coiled nucleus, and able to swim about in water by the vigorous lashing of numerous little thread-like cilia attached to one end. These are the *sperms*, or male reproductive cells (Figs. 22 and 23.)

16. Fertilization.—Neither the eggs nor the sperms are able, independently, to reproduce their kind. In order to accomplish this they must unite, and the fusion of the sperm and egg is fertilization. *One of the most significant facts about fertilization in ferns is that free water is required, in order that the sperms may reach the egg by their own locomotion.* When the antheridia and archegonia

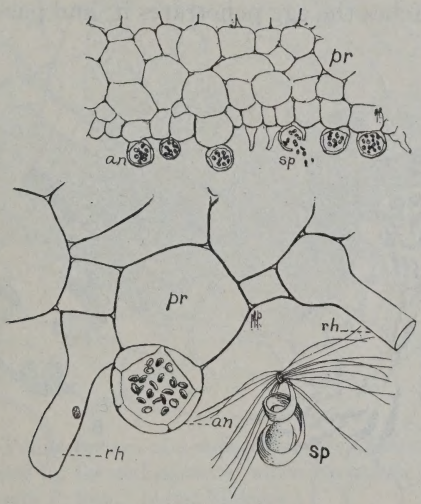


FIG. 23.—Fern prothallus; cross-sections showing antheridia (*an*), sperms (*sp*), and rhizoids (*rh*). Below at the right is a sperm (*sp*) greatly enlarged.

are mature, a suitable amount of water (such as would result from a rain or a copious dew), soaking through the archegonial walls, will cause the mucilaginous matter in the neck-canal to swell. This in turn will rupture the archegonia at their distal ends, and a portion of the contents of the neck-canal will become extruded, while the egg will remain in the venter. The same conditions of

moisture will cause the rupture of the antheridia, and the sperms will be set free (Fig. 23). The mucilaginous matter extruded from the archegonia contains a substance (malic acid, in some ferns) which stimulates the sperms to swim toward it. This they are enabled to do by the free external water. On reaching the archegonia, they enter it, and swim down the neck-canal to the egg. The sperm that first reaches the egg penetrates it, and passes through

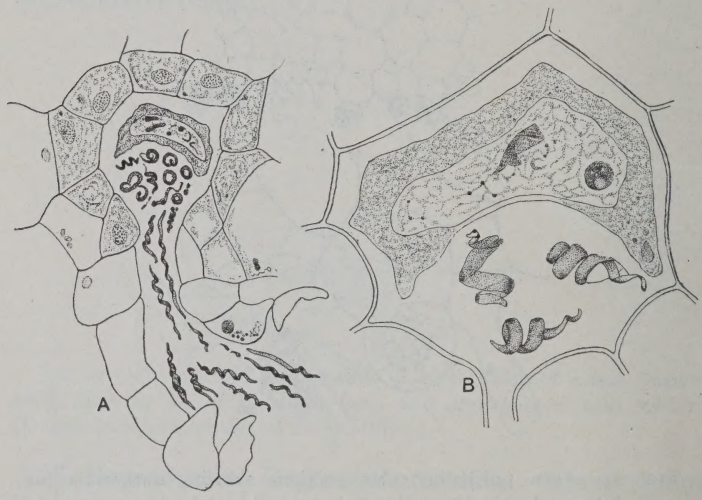


FIG. 24.—Fertilization in the fern, *Onoclea*. *A*, longitudinal section of archegonium, showing the egg in the venter, and numerous sperms passing down the neck-canal. *B*, an egg-cell in the venter. One sperm has entered the nucleus, three sperms have failed to enter the egg. (After W. R. Shaw.)

its cytoplasm until it reaches the egg-nucleus, with which it fuses, thus completing the act of *fertilization* (Fig. 24). As soon as one sperm enters the egg-cell, the latter at once forms a *fertilization-membrane* about itself, through which the remaining sperms cannot enter.

17. Nature of the Fertilized Egg.—It will at once be recognized that the fertilized egg, resulting from a union with the sperm, possesses a double or *diploid* nature.[1] In recognition of its dual nature it is called the *öosperm* (egg and sperm).[2] The öosperm, however, like the un-

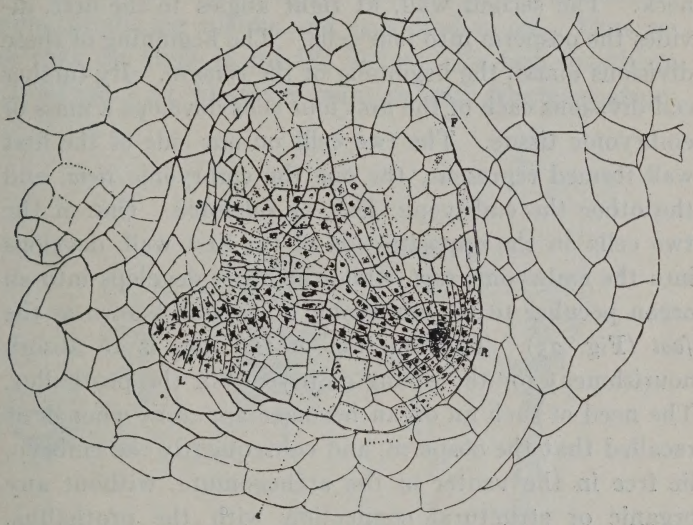


FIG. 25.—Young embryo of a maidenhair fern (*Adiantum concinnum*), still surrounded by the archegonium, which has grown in size. *L*, leaf; *S*, stem; *R*, root; *F*, foot. (After Atkinson.)

fertilized egg, is still only one cell, though its nucleus comprises substances contributed by both egg and sperm. In some cases the egg and sperm that unite in fertilization may come from different parents; their fusion is then called *cross-fertilization*.

[1] As distinguished from the unfertilized egg, which is of a single, or *haploid* nature.

[2] The term *öospore* is often used here, but this term lacks the advantage of indicating the real nature of the fertilized egg.

18. Development of the Fertilized Egg.—After fertilization the egg begins to develop, undergoing a series of nuclear and cell-divisions, accompanied by increase in size. The cell-wall of the first division (in all of the family Polypodiaceæ) is parallel to the axis of the archegonial neck. The second wall, at right angles to the first, divides the oösperm into four cells. The beginning of these divisions marks the beginning of the *embryo*. By further cell-divisions each of the first four cells develops a mass of embryonic tissue. The two cells on one side of the first wall formed represent, the one the embryonic *stem*, and the other the embryonic leaf, or *cotyledon*. One of the two cells on the opposite side of the first wall, develops into the embryonic *root*, while the other develops into an organ peculiar to the embryonic stage, and known as the *foot* (Fig. 25). The function of the foot is to absorb nourishment for the young embryo from the prothallus. The need of such an organ becomes apparent when it is recalled that the oösperm, and consequently the embryo, lie free in the venter of the archegonium, without any organic or structural connection with the prothallus. This necessary connection is early established by the foot.

19. Growth of the Embryo.—As the embryo continues to grow, the root develops first. The advantage of this will become evident when we remember that the primary and most fundamental need of the young plant is water, which is taken in by the roots. The next most fundamental need is nourishment, and as plant food is manufactured in chlorophyll-bearing organs, and usually in leaves, we would expect the early development of leaves. Such is the case, the growth of the first leaf being secondary only to that of the root, and in advance of the stem.

The development of the stem follows, and finally spore-bearing leaves appear (Fig. 26). We then have an organism similar to that with which we started—a full-grown fern-plant, capable of producing spores, which can develop into prothallia again, with antheridia and archegonia, producing sperms and eggs, and so on. Thus we see that the steps in the life history of a fern constitute a *life-cycle.* At whatever point or with whatever struc-

FIG. 26.—Prothallia of a fern. 1, Before the sporophyte had appeared; 2–5, with sporophytes attached; *l*, cotyledon or first leaf of the sporophyte; *v*, circinate vernation of a leaf; *s*, mass of soil.

ture we start, if we follow the course of development we are brought back again to the same point, or the same kind of structure with which we began.

20. Simpler Ferns.—In addition to the leptosporangiate ferns, which have served as a basis for the generalized description given above, there is another group, having a more primitive type of organization. Representatives of this group include the "moonworts" (species of *Botrychium,* Fig. 27), and the "adder's tongue" (*Oph-*

ioglossum vulgatum, Fig. 28). The species of *Botrychium* usually (though not invariably) possess but one

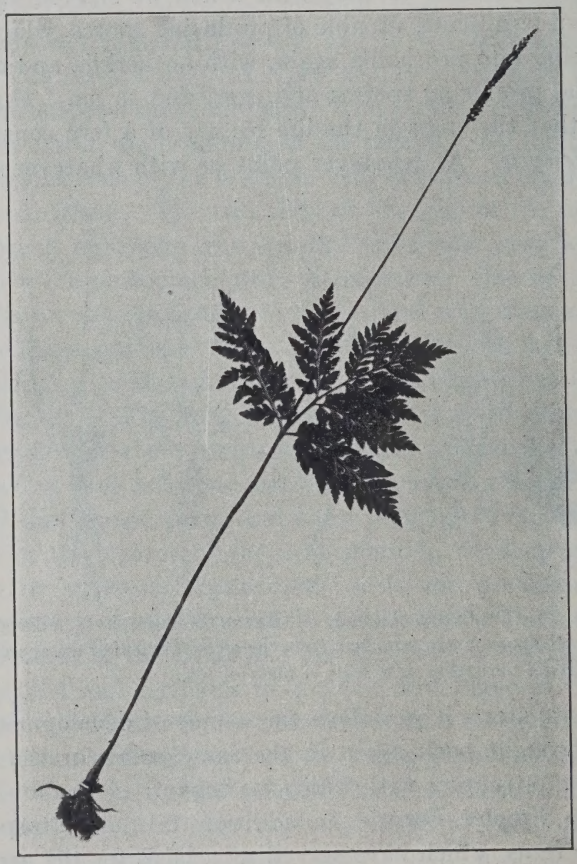


FIG. 27.—Rattlesnake fern (*Botrychium virginianum* (L.) Sw.).

foliage-leaf, and a fertile spike, both of which are more or less branched. Abnormal forms are not uncommon in which the fertile spike is more or less *sterilized*, sometimes

being entirely so; while in other cases sporangia occur on the foliage-leaf. As in the replacement of sporophylls by sterile leaves in the ostrich fern, *Onoclea struthiopteris* (paragraph 8), these abnormalities indicate the close relationship between leaves and spore-bearing organs, and clearly show that the latter may be completely transformed, by sterilization, into foliage-leaves.

In *Ophioglossum* the foliage-leaf and spore-bearing spike are both unbranched, the latter suggesting an adder's tongue, whence the name, *Ophioglossum*. In both *Ophioglossum* and *Botrychium* the sporangia originate from *a group* of epidermal and sub-epidermal cells, and are consequently imbedded in the surrounding tissue. Their walls are more than one cell in thickness, the annulus is lacking, and they open by a slit. Ferns of this type are called *eusporangiate* (*Cf.* p. 10). Their prothallia are usually fleshy and subterranean, bear the antheridia and archegonia on the dorsal instead of on the ventral surface, and are per-

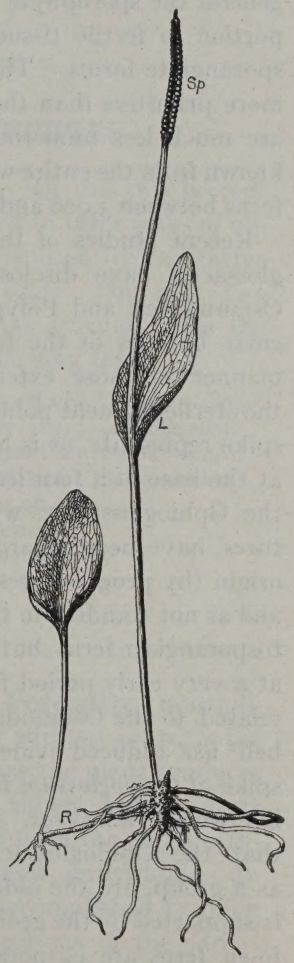


FIG. 28.—Adder's tongue fern (*Ophioglossum vulgatum* L.). *R*, runner or stolon.

ennial, often living on after the sporophyte has died. In general the sporophyte possesses less sterile tissue in proportion to fertile tissue than is the case with the leptosporangiate forms. These characters mark the group as more primitive than the leptosporangiate ferns, and they are much less numerous, only about 100 species being known from the entire world, while of the leptosporangiate ferns between 3,000 and 4,000 species have been described.

Recent studies of the vascular anatomy of the Ophioglossaceæ have disclosed features in common with the Osmundaceæ and Polypodiaceæ. The fact that the vascular bundles of the fertile spike originate in the same manner as those extending into the pairs of pinnæ of the sterile segment points to the conclusion that the fertile spike represents, or is homologous with, two fused pinnæ at the base of a fern leaf. From this and other evidence the Ophioglossaceæ, while "simpler" in structural features, have been regarded as not having had a strobilar origin (by progressive sterilization[1]) from the liverworts, and as not standing in the ancestral line of the modern leptosporangiate ferns, but as having themselves been derived at a very early period from a primitive fern stock closely related to the Osmundaceæ. On the other hand, Campbell[2] has adduced evidence for the derivation of the fertile spike of *Ophioglossum* from a sporogonium like that of the liverwort, *Anthoceros*. This and other evidence indicates that the Ophioglossaceæ, and the eusporangiate ferns as a group, are the oldest fern stock, and this conclusion is supported by the geological record, for the oldest known fossil ferns are eusporangiate. Further investigation is necessary before the question can be definitely settled.

[1] Cf. pp. 379, 432, and 574 *infra*.

[2] Campbell, D. H., Amer. Nat. **41**: 139–159. 1907.

CHAPTER III

FUNDAMENTAL PRINCIPLES

21. Two Kinds of Reproduction.—In the two preceding chapters attention has been called to three ways of obtaining new fern-plants, namely, by spores, by vegetative multiplication, and by fertilized eggs. The first two methods may be grouped together as asexual, while the second is sexual, as shown in the following table.

Reproduction	**Asexual**, involving cell-divisions only.	By the giving off of multi-cellular portions or outgrowths of vegetative tissue.	Artificial (slips, cuttings, etc.).
			Natural (tubers, bulbs, gemmæ).
		By the giving off of special reproductive bodies of one or few cells, called *spores*.	
	Sexual, involving cell-fusions.		

22. Vegetative Multiplication.—Vegetative multiplication may be accomplished either without or with the intervention of man. In the first case the plant produces special reproductive bodies such as tubers, bulbs, offsets and stolons, which become separated from the plant without assistance, and develop into new individuals. In the second case a similar result is accomplished through the removal by the gardener of portions of the parent plant, such as slips, cuttings, leaves (*e.g.*, in the begonia), or by bending branches over until they touch the ground, and there take root, after which the newly rooted portion

may be severed from the parent plant. This is called *layering*. The production of new individuals by the artificial methods of the gardener is called *propagation;* but between these methods and multiplication by special bodies, given off spontaneously by the plant, no hard and fast line can be drawn. Some plants, for example, become layered without the gardener's assistance; other plants (as the willow), by self-pruning, spontaneously give off branches from which new plants may develop; while, on the other hand, the gardener may cut a tuber, such as the "potato" into a number of pieces, from each of which a new plant will develop. In this practice artificial propagation and vegetative multiplication are combined.

23. Reproduction by Spores.—The essential fact about a spore is that it is an individual cell or small group of cells, produced primarily for reproductive purposes, given off by the plant, and capable *by itself* of producing a new individual. *The essence of all reproduction is the separation of the reproducing cell or body from the parent* plant. If a bud or a bulb remains attached to the plant that formed it, it produces only a branch or other organ, but not a new individual. So, also, a spore must be separated from the parent plant in order to *reproduce* the latter. In many cases spores may germinate before they are set free, but the separation must come sooner or later.

24. Sexual Reproduction.—In marked contrast to reproduction by spores, is the reproduction by means of sperms and eggs, *involving cell- and nuclear-fusions*, known as fertilization. Eggs and sperms are called *gametes*,[1] the egg being the *female gamete*, the sperm the *male gamete*. The diploid cell, resulting from the union of two gametes, is called a *zygote*, and this term is often extended

[1] From the Greek word, γάμος (*gamos*), meaning marriage.

to apply to the resulting diploid organism through all stages of its development to maturity.

25. Two Kinds of Generations.—A study of the life history of the fern disclosed two distinct phases or generations, one bearing spores, and therefore called the *sporophyte* (spore-bearing plant), the other bearing gametes and for that reason called the *gametophyte* (gamete-bearing plant). The gametophyte of the fern was seen to be entirely independent of the sporophyte, capable of manufacturing its own food by means of its own chlorophyll, not dependent upon any other plant, and in some groups being perennial, living on from year to year, and giving rise to sporophytes that live for only one season. The sporophyte, on the other hand, is *at first*, entirely dependent upon the gametophyte for its nutrition, living as a parasite upon the prothallus, from which it absorbs its nourishment by means of the special organ, the foot. Gradually, however, the sporophyte puts forth roots, capable of taking in water and dissolved mineral substances from the soil, and chlorophyll-bearing organs the fronds or leaves), capable of manufacturing organic food. As the sporophyte becomes independent, the gametophyte (with few exceptions, as noted above), perishes. A comparison of the two generations shows that the sporophyte is the much more complex of the two, being clearly differentiated into roots, and leafy shoot. The difference in the origin of these two generations results in a very fundamental difference in the nature of all the cells in each. Since the sporophyte is derived from an oösperm (zygote), formed by the fusion of the two, gametes, all of its cells are diploid, containing material derived from both its male and female parentage. The

gametophyte, on the other hand, being derived from a single reproductive cell (the spore), without nuclear or cell-fusions, is composed of cells of a single or haploid nature.

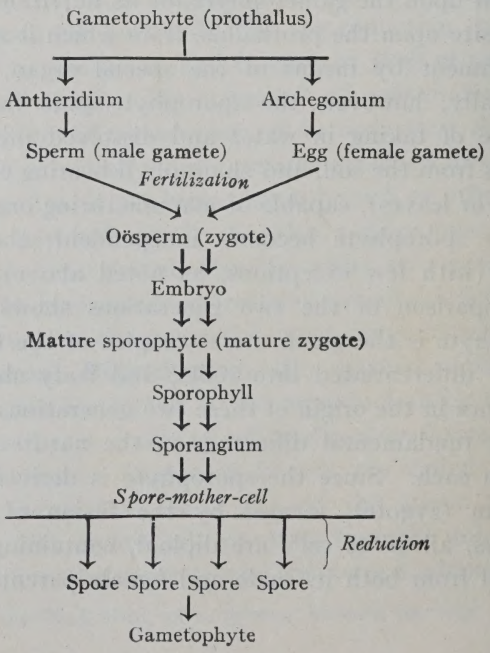
26. Alternation of Generations.—Our study of the fern also brought out another fact of very fundamental importance. Sporophytes do not produce sporophytes, nor gametophytes, gametophytes; but there is always an *alternation of generations*, sporophytes producing gametophytes, and gametophytes, sporophytes.

The order of sequence in the life-cycle is as follows:

sporophyte→spore→gametophyte→gametes→oösperm→sporophyte.

The order of structures and processes involved in the life-cycle is as follows:

OUTLINE OF LIFE HISTORY OF A FERN



The fact of a cycle in the life history is brought out clearly in the following diagram:

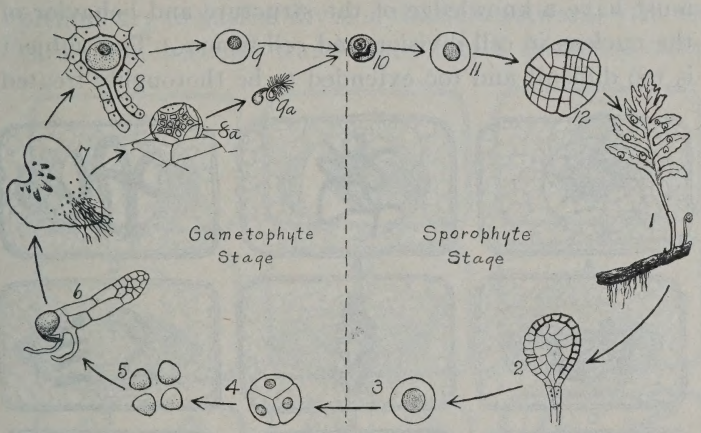


FIG. 29.—Diagram of life-cycle of a fern.

27. Reduction.—Since the sporophyte (descended from the diploid oösperm) has cells of a double nature, resulting from fertilization, and since the spores which give rise to the gametophyte are of a single (or haploid) nature, there must occur, at some stage in the life of the sporophyte, a process of *reduction*, restoring the cells, made diploid by fertilization, to the haploid condition. Painstaking studies of cellular structure and processes has disclosed the fact that this reduction takes place during the two successive divisions (tetrad-divisions) of the spore-mother-cell, resulting in the formation of four spores. The diploid condition persists in all the cells of the sporophyte, and through every cell-division, up to the two divisions preceding spore-formation, just as the single or haploid condition persists in all the cells of the gametophyte, up to the very act of fertilization.

28. Nature and Method of Reduction.—In order thoroughly to understand fertilization and reduction one must have a knowledge of the structure and behavior of the nucleus in cell-division and cell-fusion. This subject is too difficult and too extended to be thoroughly treated

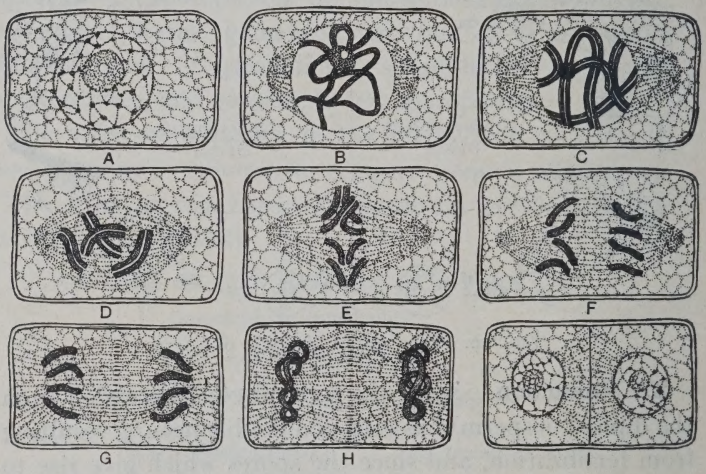


FIG. 30.—Diagram illustrating various stages of indirect nuclear division (mitosis). *A*, resting nucleus of the mother-cell; *B*, formation of nuclear skein or spirem; *C*, longitudinal splitting of the spirem; *D*, the chromosomes (four in number) have been formed by the transverse segmentation of the spirem; *E*, chromosomes arranged on the equator of the nuclear spindle; *F* and *G*, early and late *anaphase*, the chromosomes moving to the pales of the spindle; *H*, formation of daughter spirems; *I*, resting stage of the two daughter-cells.

in an introductory study, but the salient facts are as follows. The nucleus of all cells comprises at least four substances: *nuclear sap*, a threadwork of *linin*, and a substance called *chromatin*;[1] all these are enclosed by a *nuclear membrane*. In the non-dividing nucleus the

[1] Because it stains readily when treated with certain aniline dyes.

chromatin is distributed on the linin threads in the form of minute granules (Fig. 30.) At one of the stages preliminary to nuclear division the linin network, with the chromatin, becomes transformed into a thickened *skein*,

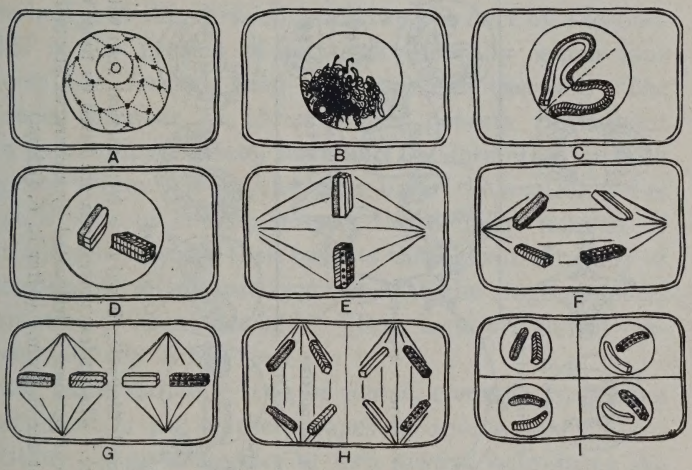


FIG. 31.—Diagram illustrating various stages in the reduction division (maiosis) of a spore-mother-cell of a plant; *A*, resting stage of the mother-cell-nucleus; *B*, the nuclear skein or spirem, in synizesis (during synapsis); *C*, the spirem after synapsis, showing its double (diploid) nature; the dotted line indicates the segmentation of the spirem into two diploid chromosomes, each of which has split longitudinally in *D; E*, the diploid chromosomes on the equator of the spindle of the first (heterotypic) division; *F*, late anaphase; *G*, metaphase of the second or homotypic division; *H*, late anaphase of same, two haploid chromosomes approaching the poles of each spindle; *I*, the four daughter-cells (spores) of the tetrad.

which shortly becomes split into two, throughout its entire length. The skein finally becomes divided transversely into a number of double chromatin bodies or *chromosomes*. The number of these chromosomes is characteristic, and always the same for each species of plant. The nuclear

membrane then disappears, and, by a complicated mechanism, not entirely understood, the two halves of the chromosomes are separated and carried apart to opposite sides

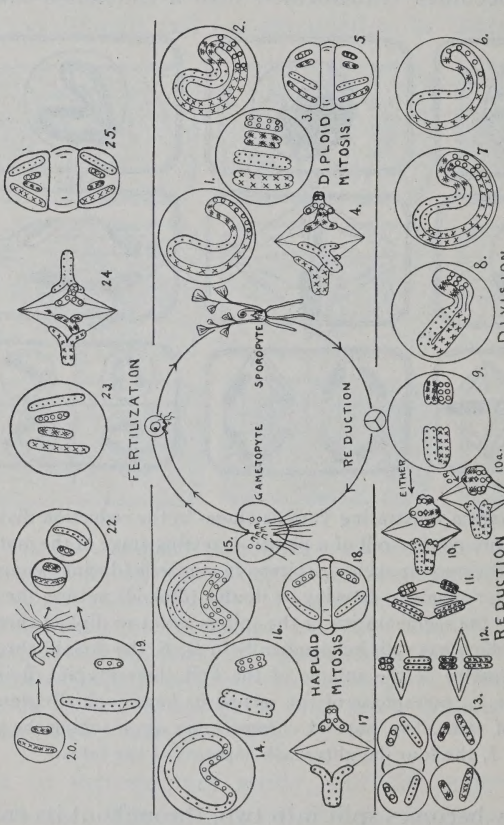


FIG. 32.—Diagram of a cytological life-cycle, based on a hypothetical fern with four chromosomes in the sporophyte. The nuclear phenomena are based on those of the thread-worm (*Ascaris*). Each chromosome is designated by a characteristic mark so that it may be traced throughout the diagram. (After R. F. Griggs.)

of the cell. After this division of the nucleus, a new cell-wall forms, dividing the entire cell into halves; new nuclear membranes develop, and the chromosomes in each

daughter-nucleus becomes gradually retransformed into a resting nucleus, like the one with which we started.

In reduction (Fig. 31) a new resting nucleus is not organized after the first nuclear division by which the number of chromosomes in each nucleus is *reduced* by one-half, but this division is followed at once by a second. This is the process of tetrad-division, by which four spores are formed from each spore-mother-cell. The reduced number of chromosomes persists throughout the gametophyte-phase, including the formation of both egg and sperm. When the latter unite, the nucleus of the zygote will, of course, possess the doubled number of chromosomes, which then persists throughout the body of the sporophyte (mature zygote), until the stage of spore-formation is again reached. These facts are shown diagrammatically in Fig. 32.

29. Inheritance.—It is, of course, common knowledge that men do not gather grapes of thorns, nor figs of thistles. A given species of fern always reproduces the same species, and this is true of all plants. It requires only a brief reflection to realize that this must be so, for the beginning of every living thing is always merely a piece of an antecedent organism, the parent. The offspring would, therefore, naturally partake of the nature of its parent—it is a piece of it—was originally a part of it. Resemblance between ancestor and descendant is commonly regarded as inheritance, but only a little careful thinking will lead us to see that *resemblance and inheritance are by no means synonymous.* The real nature of inheritance is well illustrated by the inheritance of property by a son from his father. The thing inherited is not an external appearance, but a material substance

(land, buildings, a business), which is handed from one to another. So it is in reproduction. *That which one generation of plants inherits from another is the substance of the reproductive cells*—the protoplasm of the spore, oösperm, tuber, or bulb—*plus a certain characteristic organization of this protoplasm, and the effects of its past history.*

30. Inheritance Versus Expression.—That inheritance and expression are not the same thing is plainly shown in the life history of the fern, for the gametophyte clearly derives its living matter by inheritance from the sporophyte, and the sporophyte, in turn, its living matter from the gametophyte, and yet the two generations look so little alike that men for centuries knew them both without recognizing the fact that they were merely two different phases in the life history of the same species of plant. So, often, among human beings, children may bear very little if any resemblance to their parents, but may closely resemble their grandparents. Clearly we do not inherit the color of our eyes or hair, the shapes of our noses, the peculiarities of our voices, or our mental traits from our parents, nor even from our more remote ancestors. What we do inherit is a tiny particle of protoplasm having a certain characteristic composition, structure, and past history. This protoplasm is capable, under certain combinations of circumstances, of developing into a mature organism, resembling the one from which it came, but under other combinations of circumstances the external appearance—the expression—may resemble that of the parent only a very little, or not at all. *Inheritance may therefore be defined as the recurrence in successive generations, of a similar cellular constitution.*[1]

[1] Following Johannsen, *Cf.* p. 67.

Expression of this cellular condition is greatly modified by circumstances, which are never precisely the same for any two individuals (*Cf.* p. 48).

31. Variation.—The preceding sentence explains, in part, why it is that no two individuals are ever precisely alike—precisely similar circumstances surrounding developing organisms never occur twice; that is, the environment varies. Besides this, internal changes may take place in the reproductive cells. For either one or both of these reasons, constant variation is the rule for living things. This subject will be considered more at length in Chapters V and VI.

32. Adjustment to Environment.—By the term environment is meant all the circumstances that surround a cell, tissue, or organism at any given time, or throughout its existence. The environment of tissues and organs includes surrounding tissues and organs, and the environment of cells includes the neighboring tissues and cells. *The most essential thing in the life of every plant or animal is to keep in harmony with its environment.* Every change of environment necessitates an *adjustment* on the part of the plant in order to maintain this harmony. Adjustments are most easily made when the plant is young and plastic, and especially while it is developing to maturity. If the amount of water in the soil is diminished the young plant will send its roots deeper, if light is entirely cut off no chlorophyll will form. A leaf, or the prothallus of ferns, is bilaterally symmetrical partly because the environment is uniform on all sides; the same organs have dorso-ventral differentiation largely because the environment is unlike above and below. The motility of sperms is an adjustment to water in the environment. Thus, variations in the

environment may result in different expressions of inheritance, just as variations in inheritance would be followed by differences in expression, even in an unchanging environment. In order correctly to understand a plant nothing is more necessary than to remember that its characteristics are the result, not of its inheritance alone, nor of its environment only, *but of the interaction between the two.*

33. Struggle for Existence.—In paragraph 7 attention was called to the fact that a moderate-sized fern produces each year about 50,000,000 spores. If each one of these spores ultimately produced a mature fern-plant, and if we allowed only 1 square foot of "elbow-room" for each plant, the progeny of one parent only, in one season would require at least 50,000,000 square feet, or nearly 1⅔ square miles. If each of these plants in turn, produced 50,000,000 offspring the next season, the descendants of only one fern plant would, in only two years, cover the stupendous area of over 83,000,000 square miles, or an area equal to that of the North American Continent. It has been calculated that a single plant of hedge mustard may produce as many as 730,000 seeds. If each seed developed another full-grown plant, and if the plants were distributed 73 to each square meter, there would be enough mustard plants to cover an area equal to 2,000 times the dry surface of the earth. One may easily imagine the result if all the seeds produced by one of our large forest trees were able to mature. And yet the total number of any given kind of fern, of hedge mustard, or of forest tree does not appreciably change from year to year. The reason, of course, is that not all of the spores and seeds produced are allowed to come to maturity.

The direct result of the enormous number of spores and seeds produced is a *struggle for existence*—for sufficient soil, water, light, and food to insure a healthy, mature plant.

34. Elimination of the Unfit.—As a result of variation certain individuals will succeed better than others in the struggle for existence. Those most poorly adapted to their surroundings will perish, and only the more vigorous ones—those best adjusted to their surroundings—will persist. The result of this struggle for existence was called by Herbert Spencer the "*survival of the fittest.*" What really takes place in nature is the elimination, by death, of the unfit. Darwin called this *natural selection*, implying that the result is similar to that when plant breeders select out of a progeny the best individual for further breeding. What really takes place in nature, however, is not so much the selection of the fittest, but a rejection of the unfit. Thus, among the 50,000,000 progeny of a single fern-plant, some are sure to have a weaker constitution than others; to develop a weaker root-system, less chlorophyll in their leaves, a less number of sporophylls or spores, or to be inferior in other ways. The result will be that, in the course of only a few years, the descendants of the most vigorous or otherwise superior plants will alone be left to perpetuate the race.

35. Problems to Solve.—In the preceding paragraphs we have called attention to a number of the problems which arise from the study of a fern. Some of these have been partially solved—probably none of them has been completely solved. In fact, we may say that our ignorance of life-processes greatly exceeds our knowledge. Very much more remains to be ascertained than has already been found out; for example, what is protoplasm?

Nobody really knows. We have analyzed the substance chemically, we have carefully examined and tried (but without complete success) to describe its structure. We know it is more than merely a chemical compound. It is a historical substance. A watch, as such, is not. The metal and parts of which a watch is made, have, it is true, a past history; but the watch comes from the hands of its maker *de novo*, without any past history *as a watch.* But not so the plant cell. It has an ancestry *as a cell;* its protoplasm has what we may call a physiological memory of the past. It is what it is, not merely because of its present condition, but because its ancestral cells have had certain experiences. We can never understand a plant protoplast by studying merely it; we must know something of its genealogy and its past history.

What is the origin of the sporophyte, and how did there come to be two alternating generations? What is the meaning of fertilization; what the mechanism and laws of inheritance? How did there come to be on the earth such plants as ferns? What was the origin of life? What is life? No one can give complete answers to these questions; but the purpose of the study of botany is to help fit us to seek the answers intelligently. To those who are interested in problems of this sort, nothing can be more fascinating, nor more profitable. It is the aim of the following chapters to give a brief, elementary résumé of the method employed and the results obtained during the past fifty years by investigators in their attempts to solve two of the more important of these problems, namely, the nature and mechanism of inheritance and the causes and course of plant evolution.

CHAPTER IV

HEREDITY

36. Importance of the Study.—1. *To Pure Science.*—No knowledge is more fundamental than a correct understanding of the laws of heredity. Its fundamental importance to pure science becomes evident at once when we consider that, since evolution has been accomplished by the descent of one organism from another, there have been one or more unbroken lines of inheritance from the dawn of plant life to the present. Hence, until we know the laws of heredity, we cannot fully understand expression, reproduction, development, variation, sex, or evolution.

2. *To Applied Science.*—Correct ideas concerning heredity are absolutely essential to such phases of applied science as animal and plant breeding. In the light of such knowledge the breeder can avoid making useless experiments, and can accomplish desired results more quickly, more cheaply, and with greater certainty of success.

3. *To Man.*—A correct knowledge of the principles of heredity is vital to mankind; no knowledge is more so. To realize this, we have only to reflect that our own characters are very largely the result of inheritance from our ancestors; and not only our characters, but our physical characteristics, our vigor of mind and body, our capacity for education, our susceptibility to disease, and often the actual existence of some disease within our bodies or minds.

37. Heredity Reduced to Its Lowest Terms.—We may study heredity under the very simplest conditions in the descent of one-celled organisms, such as *Pleurococcus*. This plant, a unicellular green alga, is a globule of protoplasm, containing chlorophyll, and surrounded by a cellulose cell-wall (Fig. 33). But why is it globular, why does it contain chlorophyll, why has it a cell-wall of cellulose? Why is it not elliptical, why is it not red instead of green, why does it have a cell-wall, instead of existing naked like the plasmodium of a slime-mold, why is its cell-wall of cellulose, rather than of lignin or chitin?

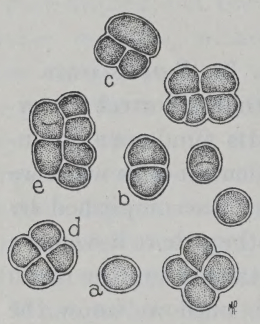


FIG. 33.—Individual plants of green slime (*Pleurococcus vulgaris*) showing the tendency of the cells to remain attached after cell-division, thus causing transitions from a one-celled to a multi-cellular plant. (*Cf.* Fig. 34.)

The short answer is, because its ancestors, for ages and ages, have possessed the characteristics which now characterize *Pleurococcus* plants. But that only puts the question back an indefinite number of generations. The real reason is, because the *Pleurococcus* protoplasm possesses a physical and chemical constitution—or in other words a mechanism—that, under normal external conditions, manufactures green pigment instead of red, cellulose instead of lignin, or any other substance, at the surface, and makes the cell-wall of even resistance to the osmotic pressure within, thus producing a sphere and not an ellipsoid, or filament, or any other shape.

38. What is Inheritance.—When the *Pleurococcus* cell divides, this wonderful, invisible mechanism—the certain

definite physical and chemical constitution—is transmitted to each of the daughter-cells; each, in other words, receives *Pleurococcus* protoplasm. *This protoplasm, with its definite organization, constitutes the inheritance.* The daughter-cells do not inherit a spherical shape (as is evident from Fig. 33), but a definite kind of protoplasm, cell-sap

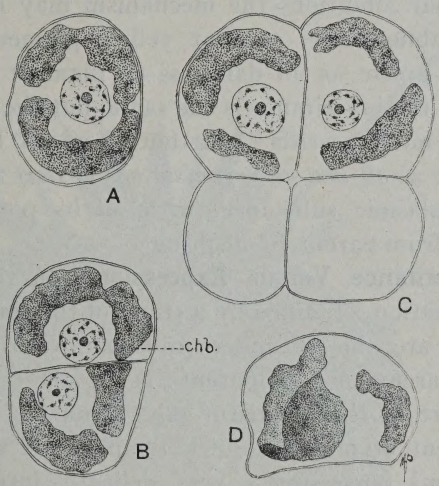


FIG. 34.—*Pleurococcus vulgaris.* Sections of one-, two-, and four-celled plants, showing the nuclei and the large chlorophyll bodies (*chb*) to which the green color of the plants is due. In *D*, the larger chloroplast is shown in perspective. (Camera lucida drawings from a microscopic preparation by E. W. Olive.). (*Cf.* Fig. 33.)

of certain osmotic properties, and surface cellulose of even elasticity, so that, in surroundings uniform on all sides, a spherical shape must finally result. The shape is an *expression of the inheritance* for the given environment. *Under different external conditions the expression might be different; but the inheritance would be the same.* The chlorophyll in the daughter-cells, immediately after cell-

division, is a direct inheritance, but the chlorophyll subsequently manufactured, and the green color which it gives to the plant, are not inherited; they are expressions of the inheritance—which in this instance is a chloroplastid (Fig. 34) that reproduces itself by division, and manufactures chlorophyll in the presence of sunlight. Under abnormal external conditions the mechanism may not act, or may act abnormally, so that yellow pigment appears instead of green—or in darkness no pigment at all. In either case the inheritance is the same, but the expression varies. A modern writer (J. Arthur Thomson) has defined inheritance as *all that an organism has to start with.* It is the protoplasmic substance, with all its potentialities, passed on from parent to offspring.

39. Inheritance Versus Expression.—In the light of this information, obtained by a study of the simple *Pleuro coccus*, we are able to understand that what we inherit from our parents or grandparents, is not a certain shape of nose, a certain characteristic gait, a musical or mathematical bent of mind, a quick temper, but *a substance* (protoplasm) possessing a very delicate, intricate, and characteristic constitution or mechanism. Under certain conditions this inheritance may so express itself as to cause resemblance in some physical or mental trait; or it may find a quite different expression, as when parents of medium height have tall children, or parents musically inclined have children that do not care for music; or sweet-peas, having white flowers only, produce, when crossed, peas having colored flowers. Or again, not all that is inherited may be expressed; this is illustrated when children resemble, not their parents, but their grandparents. Here the parents transmitted an inheritance which, in them, found no expression.

A remarkable illustration of inheritance without expression is seen in the case of the *alternation of generations* (pages 33–35). The inital protoplasm of the sporophyte is all inherited through the fertilized egg from the game-

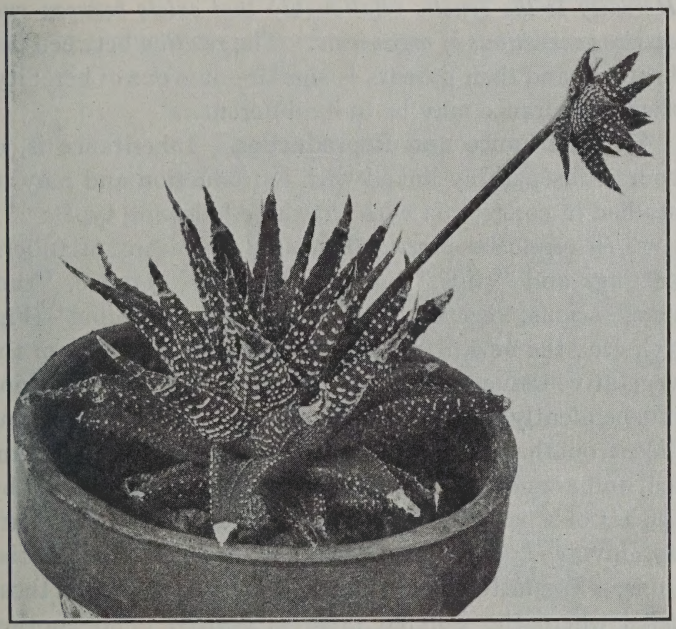


FIG. 35.—Vegetative propagation of *Haworthia sp.* The new plantlet forms on the flower stalk, below the flower-cluster. Ultimately it falls to the ground and takes root, becoming established as an independent plant.

tophytes, but most of the gametophytic characters do not appear in the sporophyte, nor do the typically sporophytic characters find expression in the gametophyte.[1] (*Cf.* p. 40.)

[1] The chlorophyll, of course, is an exception. But the osmotic strength of the cell-sap is a different expression in gametophyte and sporophyte, otherwise the young sporophyte could not live parasitically upon the gametophyte.

40. Inheritance Versus Heredity.—As stated above, *the inheritance is that which is actually transmitted* from parent to offspring. The fern-spore, for example, is the inheritance of the fern gametophyte from the sporophyte. *Heredity is the genetic relationship that exists between successive generations of organisms.* The *relation* between two brothers and their parents is similar—it is one of heredity; their inheritance may be quite different.

41. Inheritance and Reproduction.—Inheritance is, of course, inseparably linked with reproduction and may be studied in connection with the three following types:

1. *In vegetative propagation, e.g.*, by means of tubers, cuttings and "slips," bulbs and bulbils, gemmæ, "runners," scions, vegetative rejuvenation or "budding" (Fig. 35), etc., the new plant is obviously only a portion of the vegetative tissue of the parent plant, isolated and growing independently by itself. The separation of the propagating piece from the parent is often (though not always) mechanical and artificial. The protoplasm remains unaltered by the act of separation, reduction divisions of cell-nuclei are not involved, and the inheritance, except in bud-variations, is unaffected by the change. This is evident in those cases where the isolated piece is grafted upon another plant; the specific or varietal characteristics of the scion are seldom, if ever, affected by the stock. Thus, in the experiment illustrated in Fig. 36, a tomato stem was grafted upon a tobacco plant, and upon the tomato were grafted three other species—*Solanum nigrum*, *Solanum integrifolium*, and *Physalis Alkekengi*. Each species was apparently not in the least altered by this drastic change in the conditions of its life.

2. *In asexual reproduction by spores* the situation is quite similar to that in vegetative propagation, but in

certain cases there is abundant opportunity for the protoplasm to become more or less altered during the complicated changes that accompany the division of the cell-nucleus. This is notably the case in the chromosome re-

FIG. 36.—Graft of tomato (*Lycopersicum esculentum*) on tobacco (*Nicotiana tabacum*). On the tomato are grafted *Solanum nigrum, S integrifolium,* and *Physalis Alkekengi.* (Graft made by Mr. M. Free.)

duction divisions preceding spore-formation in the sporophytes of higher plants (p. 37), especially when the plant is a hybrid; and in spore-formation *in the sporangia produced from the zygospore* of some of the filamentous fungi, like *Rhizopus* or *Mucor*, the common black mold of bread. In

the latter case the nuclear divisions, some time preceding spore-production, result in separating out the female (+) and male (−) strains, so that the spores in a given sporangium are unlike as to sex—some being female (+), some male (−), (Fig. 37). This will be discussed more fully in the next chapter. Such changes result merely in distributing the heritable units (*genes*) of the mother-cell

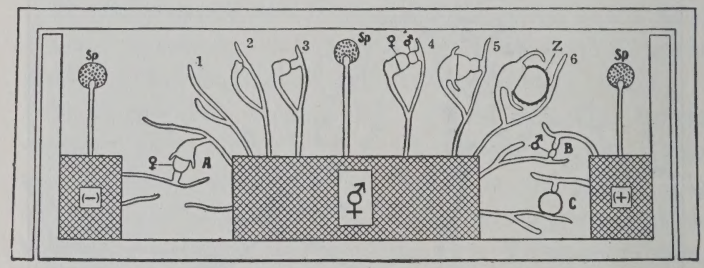


FIG. 37.—Sexual reaction between a hermaphroditic *Mucor* and (+) and (−) races of a dicœcious species. Diagrammatic representation of a Petri dish culture showing a heterogamic hermaphroditic Mucor (♂♀) in the center separated by channels on either side from the (+) and (−) races, respectively, of a dicœcious species. *Sp.*, sporangia containing spores by means of which the plant may be reproduced nonsexually. 1–6, stages in development of a hermaphroditic zygospore from unequal male and female gametes. *A*, sexual reaction between a (−) filament and a female gamete. *B*, sexual reaction between a (+) filament and a male gamete. *C*, a male zygospore formed by stimulus of contact with a (+) filament. (After Blakeslee.)

unequally to the daughter-cells, but introducing nothing new; they may, however, result in the complete loss of one or more heritable units, or in the formation of a new one, not existent in the parent. In the latter two cases we recognize a mutation. No hard and fast line can be drawn between the various kinds of asexual reproduction; there are various degrees of transition between reproduction

by spores, gemmæ, bulbs and tubers, and the artifically severed buds and scions used in grafting and "slipping."

3. *In sexual reproduction* there intervene between parents and offspring, not only the complicated reduction divisions involved in the formation of the gametes, but also the *nuclear and cell-fusions* accomplished by the union of the egg and sperm in fertilization (Fig. 38). Both processes—the formation of the gametes, and their fusion—

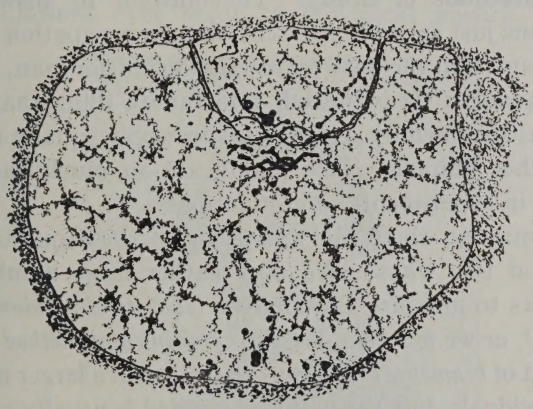


FIG. 38.—Fertilization in the white pine (*Pinus Strobus*). The smaller sperm-nucleus (above) is imbedded in the (larger) egg-nucleus. The fusion of the nucleoplasms will finally become more intimate. (After Professor Margaret C. Ferguson.)

offer almost unlimited opportunities for alterations of the protoplasm—especially that of the nucleus. This method of reproduction, therefore, has the very greatest interest and importance for the study of heredity. In the fertilized egg[1] are united inheritances from two parents—from two distinct lines of ancestry—protoplasms (germ-plasms) with two entirely different histories extending back into the

[1] The fertilized egg (as Thomson has pointed out) *is* the inheritance, and becomes, in the mature individual, the inheritor.

past, no one knows how far. How will these two inheritances affect each other when they intermingle in the fertilized egg? Will one tend to inhibit or check certain characteristics or functions of the other; will they evenly blend, so as to produce an expression intermediate between that of the parents; or may entirely new substances be formed or new combinations take place, resulting in an entirely new expression in the offspring?

42. Methods of Study.—To endeavor to answer the questions just asked is as fascinating an occupation as it is important, and the answers are significant for man, as well as for plants. It is indeed, a fortunate thing that principles ascertained by studying plants apply equally to man and other animals, since plants are so much easier to handle in experimental investigations.

We may go about the answering of these questions in either of two ways. We may gather large numbers of statistics to measure and analyze (*statistical or biometrical method*), or we may employ the *experimental method.* The method of *biometry* enables us to deal with a larger number of individuals, but the material studied is usually a mixed population, whose history is only imperfectly known, the conditions are more complex, and little if at all under control. By the experimental method it is not necessary to deal with such large numbers; we may choose carefully pedigreed material, about the history of which we have more or less accurate knowledge, and we may greatly simplify and control the conditions under which we make our observations. The largest advance toward the solution of the problems of inheritance has been made by the experimental method, in the form first employed successfully by Gregor Mendel. This method will be briefly explained in the next chapter.

CHAPTER V

EXPERIMENTAL STUDY OF HEREDITY

43. Gregor Mendel.—Two of the most important contributions ever made to biological science, namely,

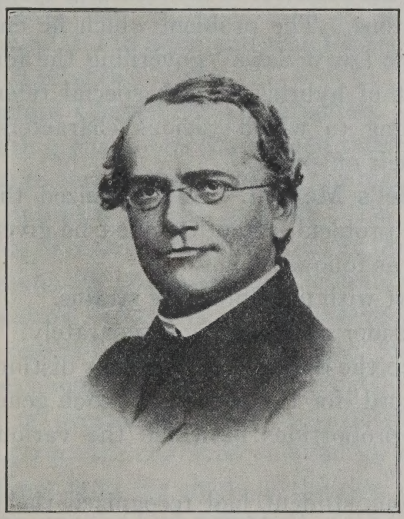


FIG. 39.—Gregor Mendel, at the age of 40. His theory of alternate inheritance (Mendelism), based largely on experiments with the garden pea, is the most important and most fruitful contribution ever made to the study of inheritance.

Mendel's laws of heredity, and his method of investigating them, were made by a teacher who studied plants as a pastime because he loved to do it. This man was Gregor

Mendel, a monk in the monastery at Brünn, Austria, where he finally became abbott. In order to understand his work clearly the student should familiarize himself the various characters of the edible or garden pea, the chief plant with which Mendel worked.

44. Mendel's Problem.—Mendel was much interested in problems concerning the origin and evolution of species. It was largely this interest that led him to *hybridize* (*i.e.*, cross-pollinate) plants of different species and varieties, and observe the behavior of the resulting *hybrids* in successive generations. The problem which he endeavored to solve was the law or laws "governing the formation and development of hybrids,"[1] with special reference to the laws according to which various characters of parents appear in their offspring.

45. Mendel's Method.—He recognized that, in order to solve the problem, attention must be given to at least four points, as follows:

1. To start with pure-breeding strains.
2. To consider each character separately.
3. To keep the different generations distinct.
4. To record, for the progeny of each generation separately, the proportions in which the various characters appear.

No previous student had recognized the fundamental importance of these requirements.

46. Choice of Material.—Mendel realized that the success of any experiment depends upon choosing the most suitable material with which to experiment. He laid down the requirements as follows:

[1] All the quotations in this chapter are from an English translation of Mendel's original paper. His form of expression has been preserved as far as possible, even when the "quotes" are omitted.

1. "The experimental plants must necessarily possess constant *differentiating characters*."[1]

2. "The hybrids of such plants must, during the flowering period, be protected from the influence of all foreign pollen, or be easily capable of such protection.

3. "The hybrids and their offspring should suffer no marked disturbance in their fertility in the successive generations."

Mendel also called attention to the advantage of choosing plants which, like the peas, are easy to cultivate in the open ground and in pots, and which have a relatively short period of growth.

47. Characters Chosen for Observation.—"Each pair of differentiating characters [have been thought to] unite in the hybrid to form a new character, which in the progeny of the hybrid is usually variable. *The object of the experiment was to observe these variations in the case of each pair of differentiating characters, and to deduce the law according to which they appear in successive generations.* The experiment resolves itself therefore into just as many separate experiments as there are constantly differentiating characters presented in the experimental plants." The following were the characters chosen for observation:

1. The difference in the shape of the ripe seeds (round and smooth *vs.* angular and wrinkled).

2. The difference in the color of the cotyledons (pale or bright yellow, or orange *vs.* light or dark green).

[1] Differentiating characters are those in respect to which the two species or varieties to be crossed differ. The possession of chlorophyll by the leaves of peas, for example, is a *common character*. "Common characters are transmitted unchanged to the hybrids and their progeny." The color of the corolla (for example, white in one species and purple in the other) is a *differentiating character*, serving to differentiate or distinguish one species from another.

3. The difference in the color of the seed-coat (white *vs.* gray, gray-brown, leather-brown, with or without violet spotting, etc.).

4. The difference in the form of the ripe pods (deeply constricted between the seeds and more or less wrinkled, or the opposite).

FIG. 40.—Method of protecting flowers from foreign pollen by paper bags, in plant-breeding experiments. (After O. E. White.)

5. The difference in the color of the unripe pods (light or dark green *vs.* vivid yellow).

6. The difference in the position of the flowers (*i.e.*, axial *vs.* terminal, on normal *vs.* fasciated stems).

7. The difference in the length of the stem (the extremes chosen were "talls" 6 to 7 feet, and "dwarfs" ¾ feet to 1½ feet in height).

48. Artificial Hybridizing.—The edible pea is commonly self-fertilized; therefore, to make crosses it is necessary carefully to remove the stamens of one flower before the anthers have begun to shed their pollen, and then place pollen from another flower on the stigma. The flowers must then be carefully guarded, *e.g.*, by tying paper bags over them (Fig. 40), to prevent other pollen being deposited by insects or otherwise. In this way the experimenter knows just what characteristics enter into the hybrid.

Careful record is kept of all data, and plants produced in this way, with ancestral characters noted and recorded, are called *pedigreed*. Plantings of such plants are called *pedigreed cultures*.

In many species, in "making the cross" (*i.e.*, doing the cross-pollinating) great care must be taken to avoid contamination from foreign pollen, of which the air may be full. The fingers and all instruments are usually rinsed in alcohol before each operation, to insure killing any foreign pollen that might be present. Numerous other precautions are also taken.

When the hybrid plants are mature, careful observations of whatever character is under observation are made and recorded. Whenever possible the observation should be quantitative.

49. Mendel's Discoveries.—We may illustrate Mendel's results in a simple manner by choosing, as the pair of contrasted characters, smooth and wrinkled seeds of the pea. Removing all the stamens from flowers of a variety having smooth seeds, he pollinated those flowers with pollen from a plant bearing wrinkled seeds.

It should now be kept clearly in mind just what the inheritance of the fertilized egg is in such a case. From the pistillate plant the inheritance, contributed by the egg-cell, included the protoplasmic properties (whatever they may be) which, when free to produce their effect, cause smooth seeds; from the staminate parent the inheritance, contributed by the sperm-cell, included the protoplasmic properties, which, when free to act, cause wrinkled seeds.

1. *Law of Dominance.*—What Mendel actually found by his experiments was that, in such a cross, all the seeds

of the hybrid plants are smooth. The inheritance was "smooth" and "wrinkled," but the expression was of only one type—smooth. A character thus expressed, to the exclusion of another, in the first filial (F_1) generation Mendel called *dominant*, and the phenomenon he called *dominance;* the other character is *recessive.* From such observations Mendel formulated the law of dominance, as follows: *When pairs of contrasting characters are combined in a cross, one character behaves as a dominant over the other, which is recessive.*

By similar experiments Mendel found that, in the cotyledons, yellow is dominant over green, tallness over dwarfness, axial flowers over terminal, and so on. Such pairs of contrasting characters are called *allelomorphs.*

2. *Law of Segregation.*—But what will happen if the first filial (F_1) generation is inbred or self-pollinated. Its inheritance included factors that make for both "smooth" and "wrinkled," but the expression was of one kind only. The experiment was made, and Mendel found that the second filial (F_2) generation included plants, part of which possessed only smooth seeds, while the others had only wrinkled seeds (Fig. 41). "Transitional forms were not observed in any experiment." This illustrates in a striking way the difference between inheritance and expression, for a character cannot appear in a plant (or animal) unless the plant possesses the factor or factors for that character. Now, except for the comparatively rare cases where mutation occurs, the factors in the F_2 generation must have been derived by inheritance from the germ-cells of the F_1 generation; but the experiment shows that they did not come to expression there. The same law is illustrated in the crossing of a sweet variety of maize (having wrinkled

grains) with a starchy variety (having smooth grains). In this cross starchiness is dominant over sweetness (Fig. 42).

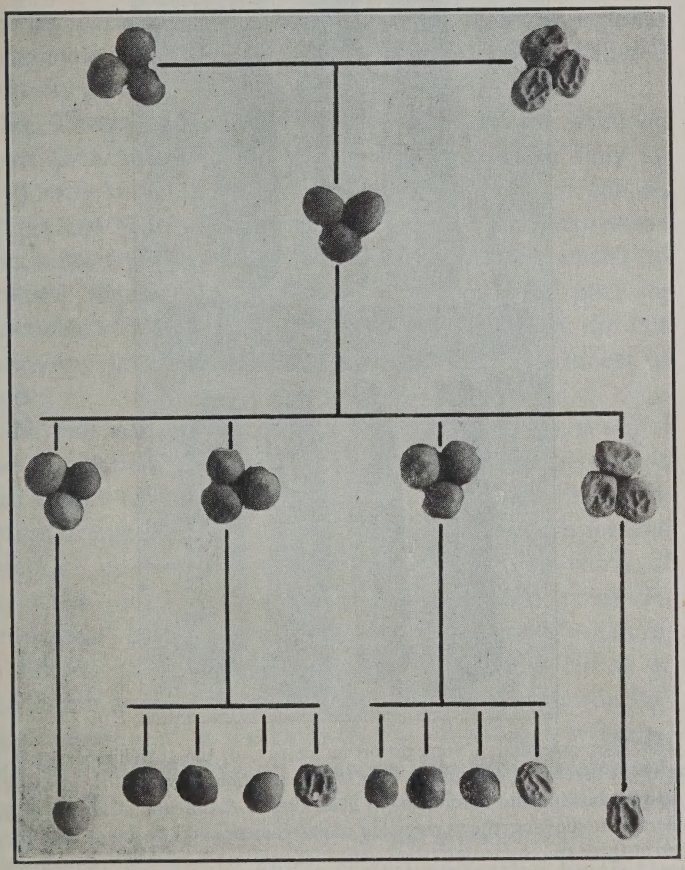


FIG. 41.—Mendelian segregation in the edible pea (*Pisum sativum*) Full explanation in the text. (*Cf.*, Fig. 42.)

50. Ratio of Segregation.—But now we come to that feature of Mendel's experiments which, perhaps more than

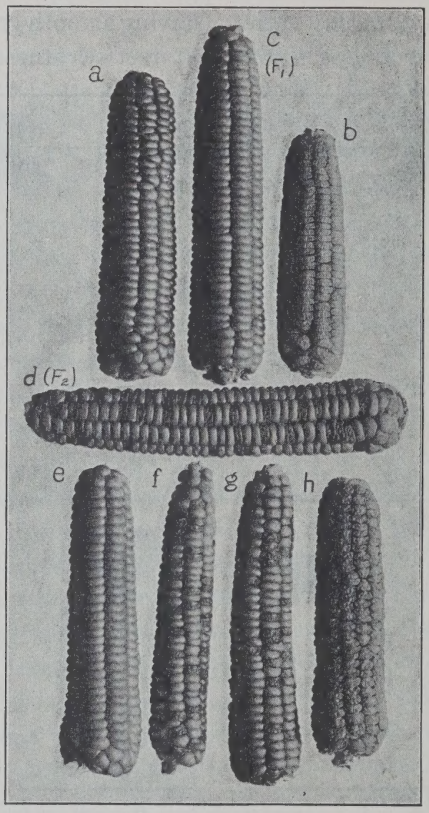


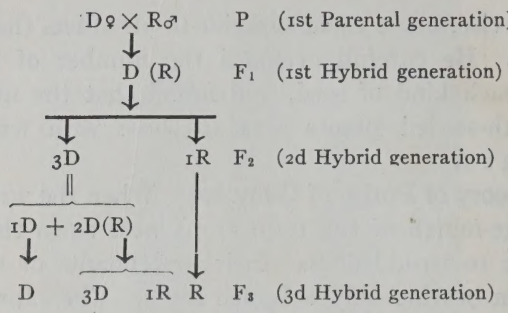
FIG. 42.—Mendelian segregation in maize. *a*, the starchy parent; *b*, the sweet parent; *C*, the first hybrid (F_1) generation, produced by crossing *a* and *b*, showing the dominance of starchiness; *d*, the second hybrid (F_2) generation, showing the segregation of starchiness and sweetness with the ratio of three starchy to one sweet (wrinkled) grain. Lower row, daughters of *d*; *e*, *f*, and *g* resulted from planting starchy grains. One ear in three is pure starchy, the other two mixed; *h*, result of planting sweet (wrinkled) seed. They are pure recessives, and the ear is pure sweet. (After East.) (*Cf.* Fig. 41.)

anything else, made them superior to all others that had preceded. He carefully *counted* the number of plants bearing each kind of seed, and found that the number of smooth-seeded plants was to those with wrinkled seeds as 3 : 1.

51. Theory of Purity of Gametes.—When the wrinkled seeds (one-fourth of the total crop) were sown they all bred true to wrinkledness—their descendants of the F_3 generation bearing only wrinkled seeds. The expression was alike in every case. The gametes that united to produce these plants were therefore considered pure *for "wrinkledness;"* that is, it was inferred that they did not carry any inheritance tending to produce smoothness of seed.

52. Not All Dominants Alike.—But when the seeds of the F_2 plants, having only smooth seeds, were sown it was found that *the dominants were not alike*, except in external appearance. The seeds, though all appeared smooth, carried different inheritances. One-third of them (*i.e.*, one-fourth of all the seed produced by the F_2 generation) bred true to smoothness, being therefore pure, or homozygous *for smoothness;* the other two-thirds of the dominants (*i.e.*, one-half of all the seed produced) again segregated in the ratio of 3:1—one-fourth wrinkled and three-fourths smooth, showing that they were *heterozygous;* that is, that they still carried inheritance from both the wrinkled and smooth-seeded grandparents.

If we designate the first parental generation by P, the dominant character (whatever it may be) by D, and the recessive character by R, then the facts above described may be diagrammed as follows:


D♀ × R♂ P (1st Parental generation)
D (R) F1 (1st Hybrid generation)
3D 1R F2 (2d Hybrid generation)
1D + 2D(R)
D 3D 1R R F3 (3d Hybrid generation)

53. Significance of the Mendelian Ratio.—The ratio 3 : 1 or, as it appears on analysis, 1 : 2 : 1, is the ratio that one might expect, or that might be predicted, on the basis of chance. Students of algebra will recognize in it the essence of the familiar square of $a + b$, namely, $a^2 + 2ab + b^2$, where a and b each equal 1. In the plants the multiplication of inheritances (produced in fertilization) was as follows:

$$\text{eggs } (s + w) \times \text{sperms } (s + w) = ss + 2sw + ww$$

where w = wrinkling and s = absence of wrinkling, *i.e.*, smoothness.

54. Theory of Purity of Gametes.—The above ratio is what we would expect if half of the egg-cells and half of the sperm-cells in a heterozygous plant (one of the F_1 generation), carried only character-units or determiners[1] that make for smoothness; the other half only those factors that make for wrinkling, giving s and w egg-cells, and s and w sperm-cells *in equal numbers*. Therefore, in pollination the chances would be equal that an s-egg would

[1] The substance or condition (protoplasmic constitution), whatever it is, in the germ-cells that corresponds to any given character of the plant is variously referred to by the terms *factor*, *determiner*, *gene* (= producer), *character-unit*, and others. These terms are essentially synonyms.

be fertilized with either an *s*-sperm or a *w*-sperm, giving $(s + w) \times (s + w) = ss + 2sw + ww$. Since *s* is dominant over *w* the product should be written:

$$ss + s(w) + s(w) + ww$$

giving *in external appearances* $3s + 1w$. Since the result actually observed is what it would be *if* the gametes were thus "pure" *for smoothness and wrinkling*, Mendel concluded that they really are, and moreover that each *character* behaves as a unit, appearing and disappearing in its entirety.

55. Character-units versus Unit-characters.—As just stated, Mendel held that the various visible characters of his plants (dwarfness, for example) behaved as units, either appearing in their fullness, or not appearing at all. From more careful observations we know that such is not the case. A blossom may, for example, be more or less pink, an odor more or less strong, dwarfs are not all the same height, but fluctuate around a mean. We conclude therefore that characters do not behave as units, and that the conception of "unit-characters" is erroneous. The evidence does, however, seem to justify the conclusion that the factor or factors, whatever they may be,[1] that are causally related to the given character do behave as units. We may therefore designate them as *character-units*. Since they are causally or genetically related to the character they have been called *genes* (from the root of the Greek word, *genesis*). They are more commonly known as *factors*. Quite probably, in many if not all cases, more than one factor is involved in the production of any given character.

[1] Substance or condition, we know not what, within the germ-cells.

56. Applications of Mendel's Law.—Over 100 pairs of structural and color characters have been found, in plant breeding, to behave more or less closely in accordance with the Mendelian conception. In peas alone over 20 pairs of characters are expressed in successive generations, in accordance with this law. Among the more striking results which are explainable upon Mendelian theory are the following:

1. Mottled beans have been produced in the F_1 generation by crossing two varieties, neither of which had mottled seeds. Various types appeared in the F_2 generation.

2. Jet black beans have appeared in the F_1 generation from a cross between two varieties, one of which had pure white seeds, the other light yellow. Various shades and colors appeared in the F_2 generation.

3. In one case three distinct varieties of beans, breeding true to white seeds (when selfed[1]), were crossed with the same variety of red bean. In the F_1 generation each cross gave a different color—one blue, another black, and the third brown. A varied assortment of colors appeared in each case in the F_2 generations.

4. Two varieties of sweet peas, each breeding true to white flowers, when crossed gave, in the F_1 generation, nothing but purple-flowered offspring, resembling the wild sweet pea. A medley of white, pink, purple, and red-flowered plants appeared in the F_2 generation. Numerous other cases might be cited, all of which would have been unsolvable riddles except in the light of Mendelism.

57. Inheritance and Environment.—Emphasis should be laid on the fact that the behavior of any plant, and the

[1] The pollination of a flower with its own pollen, or with pollen from another flower of the same plant, is called *selfing*.

characters it manifests, are the result of the combined influence of inheritance and environment. A bean seedling is green, not merely because it has inherited chloroplastids, but because it develops in sunlight; without sunlight the green color could not come into expression. If we vary any factor of environment (temperature, moisture, illumination, food) the expression of the inheritance may be altered, just as truly as though the inheritance were changed. *The characteristics expressed by any plant (or animal) are the result of the combined action of inheritance and environment.* It is of fundamental concern to a man, not only to be "well-born" (*eugenics*), but also to be "well-placed" (*euthenics*), although the former, according to present day conceptions appears to be more important.

58. Johannsen's Conception of Heredity.—The conception that inheritance, as previously noted, is not the transmission of external characters from parent to offspring, but the reappearance, in successive generations, of the same organization of the protoplasm with reference to its character-units, was first developed by Johannsen, of Copenhagen, Denmark, who proposed the term "genes." "The sum total of all the 'genes' in a gamete or zygote," is a *genotype. Inheritance is the recurrence, in successive generations, of the same genotypical constitution of the protoplasm.* Johannsen does not attempt to explain the nature of the genes, "but that the notion 'gene' covers a reality is evident from Mendelism." This conception of heredity is diametrically opposed to the older and popular conception, but is much more closely in accord with the facts revealed by recent studies of plant and animal breeding (*Cf.* p. 40).

59. Pure Line Breeding.—Johannsen also originated the "pure line" theory—a theory which has done much toward elucidating the problems of selection. He and his followers regard genetic factors as fixed and unvarying. Hence the results obtained in selective breeding of a given variety of maize for high or low oil content, or of a given variety of beans for larger or smaller size of seed, would be interpreted on this theory, as the isolation or separation of pure strains from a "mixed population" or "impure" variety. In practical language, several true breeding varieties of beans, differing in seed size, might be obtained by selection from what appeared to be a "pure" variety with considerable variation in size of seeds.[1]

60. Value of Mendel's Discoveries.—The discoveries that, in inheritance, certain characters are dominant over certain others; that a given inheritance (*e.g.*, conditions associated with seed-color, odor, eye-color, stature, musical ability, insanity, tendency to some disease) may be carried and transmitted to offspring by an adult who gives no outward signs of carrying the inheritance; that, under certain conditions of breeding, some characters (the recessive ones), whether good or bad, may become permanently lost; that dominant characteristics are certain to reappear in *some* of the offspring—all of these truths, learned by the study of a common garden vegetable, will be recognized at once as of enormous importance to the breeders of plants and animals, and above all to mankind, in connection with our own heredity. They point the way to the explanation of such enigmas as the proverbial bad sons of pious preachers, spendthrift children

[1] A detailed discussion of Johannsen's method of "pure line" breeding belongs to more advanced studies.

of thrifty parents, talented offspring of mediocre parents, blue-eyed children of brown-eyed parents,[1] and so on.

61. Increased Vigor from Crossing.—Experiments with pedigreed cultures have disclosed a principle of the utmost practical importance for the plant breeder. A careful analysis of a field of Indian corn (*Zea Mays*) has disclosed the fact that any given variety is very complex, being heterozygous for many characters; in other words any horticultural variety is a composite of numerous elementary species, and is therefore heterozygous for most of its characters. When pollination is allowed to take place in the corn field without interference by man, both crossing and selfing occur. As a result the yield, in bushels per acre, remains about stationary, or gradually becomes less and the variety changes and deteriorates by the segregation and recombination of the numerous elementary species that compose it.

By artificial self-pollination for several generations (*e.g.*, (five or more) less complex strains result, which are homozygous for one or more characters, and the yield per acre may thus become greatly reduced.[2] If now, two of these simplified strains, homozygous for many characters, and

[1] If both parents have blue eyes the children with rare exceptions have blue eyes; if one parent has brown eyes and one blue, the children may be both blue- and brown-eyed, or all brown-eyed, for brown eye-color tends to be dominant over blue color. When both parents have brown eyes, part of the children may have blue eyes and part of them brown, or they may all be brown-eyed. As used here, the term "brown-eyes" means all eyes having brown pigment, whether in small spots (gray eyes), or traces (hazel eyes), or generally distributed (brown, or sometimes black, eyes). The term "blue eyes" designates only those cases in which brown pigment is entirely lacking.

[2] If a high-yielding strain was separated out by selection, the yield would of course be increased above the average of the mixed field.

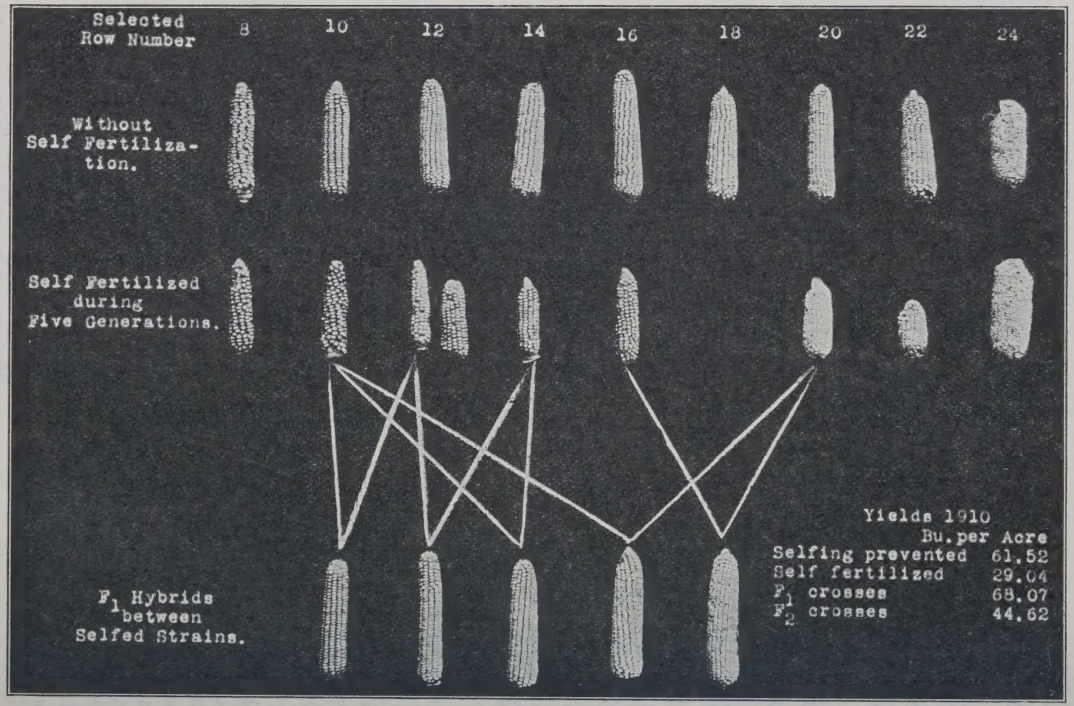

Selected Row Number
8
10
12
14
16
18
20
22
24
Without Self Fertilization.
Self Fertilized during Five Generations.
F1 Hybrids between Selfed Strains.
Yields 1910
Bu. per Acre
Selfing prevented 61.52
Self fertilized 29.04
F1 crosses 68.07
F2 crosses 44.62

FIG. 43.

having a low yield per acre, are crossed, there results an F_1 hybrid progeny that is heterozygous for all of these characters. This heterozygosity is correlated with a greatly increased vigor; the plants are much larger, and the yield per acre is enormously increased (Fig. 43). Thus in one experiment of this kind the average yield of the heterozygous horticultural variety was 61.25 bushels per acre. After self-fertilization for several generations the yield became reduced to 29.04 bushels per acre; but in the F_1 generation of a cross between two of these self-fertilized strains the yield per acre rose at once to 68.07 bushels. In the F_2 generation the yield again fell to 44.62 bushels. From this, and numerous other experiments, it is found that the biggest corn crop is to be obtained by finding the strains that will produce the largest yield when crossed, and then using for seed the grains of the first-generation hybrids each year.

62. Breeding for Disease-resistance.—Biffen, in England, crossed a wheat of poor quality, but resistant to rust disease (*Puccinia glumarum*), with a superior variety but very susceptible to the disease. Susceptibility proved dominant in the F_1 generation, but in the F_2 generation disease-resistant forms appeared, of superior

FIG. 43.—*Zea Mays*. In the experiment, the results of which are here illustrated, nine strains of Indian corn were selected according to the number of rows of kernels on the cob, varying from 8 to 24 rows. These were pollinated by hand each year, with mixed pollen, in such manner that self-pollination was entirely prevented. An average ear of each strain is shown in the first row above. In the second row is shown an average ear of each strain after self-fertilization for five generations. Note the resulting decrease in the number of rows, lack of filling out of the ears, and other marks of inferiority. The last row shows the remarkable and immediate increase of vigor resulting in the F_1 generation of hybrids between various pairs of the selfed strains. (Photo supplied by G. H. Shull.)

quality, which bred true for resistance. The watermelon, in the southern states, is subject to a very destructive disease which causes a wilting of the vines and consequent loss of fruit. By crossing the ordinary non-resistant watermelon with the closely related common citron, which is wilt resistant, W. A. Orton, of the United States Department of Agriculture, produced a watermelon resistant to this disease. Numerous other illustrations might be given. This is becoming one of the common and successful methods of combating plant disease.

63. Unsolved Problems.—Like all truly great contributions to science, Mendel's discoveries have raised more questions than they have answered. Therein lies, in part, their great value. So, also, the most important effect of Darwin's work was that it set men to asking questions. The history of botany, as of all natural science since 1859, is chiefly the attempts of men to answer the questions raised by Darwin, or stimulated in their own minds by his books. So with Mendel and de Vries; biological science, since 1900, has been largely occupied in trying to answer the questions raised by these men.

What are these questions? There is not space here even to ask them all, much less to endeavor to answer them even briefly; but they include the following large problems:

1. *Are acquired characters inherited?* In other words, do characteristics acquired after birth by the body or mind of the parent, either by its own activity or as a result of the immediate effects of environment, influence the germ-cells so as to alter the inheritance which they transmit? Some say yes, others say no; others say, only

in part. There seems to be evidence both ways, but the bulk of the evidence and the weight of scientific opinion is against the inheritance of acquired characters as here defined. We can arrive at the correct answer only by careful experimentation, that is, by asking questions of nature.[1]

2. *Can the inheritance of a strain be artificially altered?* This is a question of the very first importance. If the inheritance could be so altered the marvels that breeders might perform would be greatly increased. A blue rose (the despair of all plant breeders) might possibly be produced by sufficiently careful and extended experimenting; disease and undesirable traits of character might be eliminated from certain tainted family strains by artificial treatment. On the other hand, by an unfortunate combination of circumstances, most undesirable and regrettable results (*e.g.*, a weed poisonous to cattle, or a new and virulent disease-causing bacterium) might be experimentally produced. The experiment has been made of exposing the ovaries of flowers to the rays of radium, and of injecting them with various chemical substances, with an idea of altering the physical or chemical nature of the egg-cells, and thus altering the inheritance. The results of such experiments, so far tried, need to be further confirmed before we can say with certainty that the result sought has been accomplished.

3. *How may dominance be explained?* Why is tallness dominant over dwarfness, brown eye-color over blue, any one character over any other? At present we can only speculate on these questions.

4. *What is the mechanism of inheritance?* In other words, by what arrangement and interaction of atoms

[1] On the inheritance of acquired characters, see Thomson, J. A., *Heredity*. London, 1908. Chapter VII.

and molecules is it made possible that the peculiar tone of one's voice, the color of a rose, the odor of a carnation, the evenness (or otherwise) of one's disposition, may be transmitted from one generation to another? How may it be transmitted *through* one generation, without causing any external expression, and reappear in the second generation removed? Is the cytoplasm the carrier, or the chromatin, or both combined, or neither? Is the transfer accomplished by little particles (*pangens*), as de Vries contends, or by chondriosomes, or otherwise? We do not definitely know, but many careful investigations point to the chromatin as the bearer of the hereditary factors.

64. Weismannism.—It was a botanist, Nägeli, who first recognized and clearly stated that inheritance must depend upon a least quantity of matter, and numerous experiments by both botanists and zoologists soon made it evident that the hereditary substance is in the cell-nucleus, rather than in the cytoplasm surrounding the nucleus. Nägeli called the hereditary substance *idioplasm.* Observations of the germ-cells of plants by Strasburger, and of the germ-cells of animals by O. Hertwig, led them to conclude that the chromosomes of the dividing nucleus (Fig. 30)are the locus of the hereditary substance. The subsequent evidence upon which this conclusion rests is too voluminous, and some of it too technical, to be presented here in any detail.[1] As an illustration there may be cited the experiment of Boveri who removed the nucleus from the egg-cell of one species of sea-urchin, and then caused the remaining cytoplasm to be fertilized with a sperm-cell of another species of sea-urchin; the resulting larva possessed *only paternal characters.*

[1] See Morgan, T. H. The physical basis of heredity. Philadelphia, 1919.

Weismann expanded the above conception of hereditary substance by calling attention to the fact that it must contain elements, not only from one individual or pair, but from a long line of ancestors. He called the idioplasm (of Nägeli) in the germ-cells *germ-plasm*, and the hereditary units, "necessary to the production of a complete individual," he called *ids*. Each id contains a full complement of hereditary factors necessary to produce a perfect plant or animal. The germ-plasm corresponds to the deeply staining *chromatin* of the cell-nucleus, and the ids are grouped together in *idants*, which correspond, in general, to the chromosomes. Weismann further postulated that the ids were composed of "primary constitutents," which he called *determinants*, and that every character independently inherited has its own determinant in the germ-plasm. Finally Weismann postulated that each determinant is a complex of *biophors* (the ultimate units of matter in the living state), each biophore being composed of (non-living) chemical molecules. Thus we rise through his categories as follows, from atom to molecule, from molecule to biophore, from biophore to determinant, from determinant to ids, from ids to idants (chromosomes), which are composed of the hereditary substance or germ-plasm; schematically as follows:

germ-plasm (chromatin)
idant (chromosome)
id.
determinant (*factor*, of Mendel)
biophore (*biogen*, of Verworn)
molecule
atom

The germ-plasm is continuous from generation to generation, and therefore possesses a kind of physical immortality.

65. Relation of Weismannism to Mendelism.—It will readily be recognized that the "determinants" of Weismann are the "factors" of Mendelian nomenclature. Morever, it follows logically from Weismann's theory that acquired characters are not inherited, an inference that agrees with observation and experiment. Nägeli, director of the botanic garden in Munich, transplanted specimens of Hawkweed (*Hieraceum*) from the high Alps to the lower altitude and changed climate of his garden, and these plants began to manifest new characters which reappeared in successive generations for more than a decade. This looked like the inheritance of acquired characters, but when the plants were subsequently taken back to the high Alps, they failed to manifest the characters expressed in the botanic garden, reverting to their former alpine characteristics. Thus it is seen that the reappearance of the new characters in successive generations in the botanic garden was not due to inheritance of these acquired characters, but to the continuity of the new environment. The inheritance had not been altered though the expression of it had. This is in agreement with what we should expect from the definition of inheritance given on page 50.[1]

66. Eugenics.—Students of biology have been quick to recognize the fact that, if we correctly understand the laws of heredity, we are in a position to apply them, not only to plants and the lower animals, but to mankind. *The application of the laws of heredity in a way to produce a healthier and more efficient race of men constitutes the practice of eugenics.*[2] The underlying principles of eugenics

[1] See also pages 48 and 66–67.

[2] The word eugenics is from two Greek words meaning *well born.*

are of course, very largely those of heredity. Eugenics is the *applied science* based upon the *pure science* of heredity. The main problem of eugenics is how to eliminate human beings with a tendency to any physical or mental weakness making for poverty, misery, ignorance, and crime; and how to increase the number of individuals physically, mentally, and morally more robust and sound; and withal how, if possible, to raise the standard of all desirable human traits. A careful study of heredity and eugenics will make possible a much more intelligent and efficient program for charity work and social betterment.

67. Investigations Since Mendel.—It must be remembered that Mendel's most valued contribution was not the observations which he made and recorded concerning the garden pea, nor the hypotheses which he advanced on the basis of those observations, but this *method of procedure*, whereby he elevated the study of heredity to the rank of an exact science. As in the case of all hypotheses, the task for science is to subject them to the most searching tests, to see if they invariably agree with facts, and may be accepted as in all probability embodying the actual truth—may be elevated to the rank of theories. The testing of Mendelism has been occupying all the best talents of many investigators since the rediscovery of Mendel's publication, about 1900. Many biologists are still skeptical, a few reject the hypotheses, and still others believe they contain the germ of truth, but must be more or less modified. *Whether they prove to be erroneous or true is not so important, but it is important for us to know which is the case.* True or not, they, like nearly all working hypotheses (natural selection, mutation, nebular hypothesis, atomic hypothesis

in chemistry, etc.) are rendering, or have rendered, a priceless service to science by pointing the way to further study, which enriches our knowledge of the living world, including ourselves, and therefore increases the intelligence with which we may order our own conduct and lives. If the study of plants had rendered no other service to mankind than this contribution of an effective method of ascertaining the laws of heredity, it would have amply justified all the arduous labor that men have devoted to it for 2,000 years.[1]

[1] Only one of the simplest cases worked out by Mendel is summarized in this chapter. A more thorough study of his experimental results and theories must be reserved for more advanced study.

CHAPTER VI

EVOLUTION

68. Doctrine of Special Creation.—In the time of Linnæus, the "father of botany," men believed that the seven "days" of creation left the world substantially as we now find it. The stars and planets, mountains and oceans, plants and animals were created once and for all, and continued without important change until the present. In the beginning, as now, there were the same oceans and hills, the same kinds of plants, and the same kinds of animals. Nor, it was believed, are any fundamental changes now in progress. Creation was not continuous; it took place within a brief period (seven "days"), and then ceased; after that the Creator merely watched over the objects of his handiwork. Opposed to this doctrine is the theory of evolution.

69. Meaning of Evolution.—Evolution means gradual change. Applied to the natural world the theory of evolution is the direct opposite of the doctrine of special creation. It teaches that things were not in the beginning as we now find them, but that there has been constant though gradual change. Creation is regarded, not as having taken place once and for all, but as being a continuous process, operating from the beginning without ceasing—and still in progress.

70. The Course of Evolution.—The theory teaches that the gradual changes have been from relatively simple conditions to those more complex. The compli-

cation has been two-fold: (1) simple individuals, whether mountains, rivers, planets, animals, or plants, have become more complex (*e.g.*, compare the structure of the plant, *Pleurococcus*, a simple spherical cell, with that of the fern); (2) the relation between living things, and between them and their surroundings has become more complex (*e.g.*, compare a unicellular bacterium, with its relatively simple life relations, with the clover plant, highly organized, and related to water, air, soil, light, temperature, gravity, bacteria (in its roots), and insects (for cross-pollination)).

Most of the steps of evolution have been *progressive*, toward higher organization, greater perfection of parts, increased efficiency of function, as, for example, from algæ having one or a few cells only, to flowering plants, like roses and orchids; but not all the steps have been in this direction. Some of the steps have been *regressive*, toward simpler organization, less perfection of parts, decreased efficiency of function, as, for example, from green algæ to the non-green, alga-like fungi (Phycomycetes, such as bread mold), from independence to parasitism (mistletoe and dodder), or to saprophytism (Indian pipe and toad-stools).

The thirty odd species of the Duckweed family, related to the Arum family (Jack-in-the-pulpit, calla, skunk cabbage, sweet flag, etc.), illustrate regression; they comprise the simplest, and some of them the smallest of all flowering plants. The plant body of *Lemna* is a tiny disc-shaped, thallus, having a central vein (vascular strand) with or without branches. Each plant has one root with no vascular tissue. The flowers, borne on the margin or upper surface of the thallus, have one simple pistil and only one stamen (Fig. 44). The dozen or more species

of *Wolffia* possess still simpler bodies, somewhat globose, with neither roots, veins, nor other organs, except flowers; even flowers are unknown in some species (*e.g.*, *Wolffia populifera*, Fig. 44). *Wolffia punctata* measures only 0.5–0.8 mm. long. The plants are fittingly described in the manuals as "minute, alga-like grains," floating on or

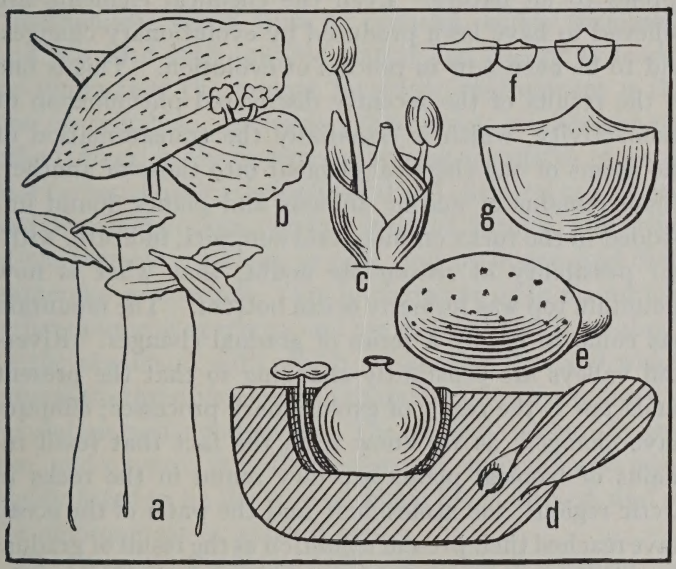


FIG. 44.—Lemnaceæ. *a*, *b*, *c*, *Lemna trisulca; d*, *Wolffia punctata; e*, *f*, *Wolffia papulifera.* (Redrawn from Britton and Brown, slightly modified.)

just beneath the surface of still water. Some botanists consider the plant body as morphologically a frond, others as a leafless stem. Since the first plant-body from the seed is only a matured cotyledon, or seed-leaf, Goebel considers that it cannot be interpreted as other than a *free-living leaf*. These tiny, simple plants are considered to have

originated by regressive evolution, their simplification being closely correlated with a reversion from dry land to an aquatic habit of life. A similar reduction of structure is found in the tiny floating ferns, *Salvinia* and *Azolla*.

71. Inorganic Evolution.—The process of evolution is not confined to living things, but, as indicated above, applies to all nature. Even the chemical elements are believed to have been produced by evolutionary changes, and to be even now in process of evolution. This is one of the results of the recently discovered phenomenon of radioactivity, which is essentially the transformation of the atoms of one chemical element into those of another. Fossil remains of marine animals and plants, found imbedded in the rocks on mountain summits, indicate, without possibility of reasonable doubt, that what is now mountain top was formerly ocean bottom. The mountain has come to be, by a series of gradual changes. Rivers and valleys are constantly changing so that the present landscape is the result of evolutionary processes; climates have changed, as we know from the fact that fossil remains of tropical plants are now found in the rocks in arctic regions; the atmosphere and the water of the ocean have reached their present condition as the result of gradual transformations extending over aeons of time; even the stars and planets, like our own earth, are coming gradually into being, undergoing changes of surface and interior condition, and ceasing to exist. *Nothing is constant except constant change.* The main problem of astronomy is to ascertain and record, in order, the evolutionary changes that have resulted in the present system of suns and planets. The main problem of geology is to ascertain and record, in order, the evolutionary steps that have resulted in the present condition of the earth.

72. Fitness of the Environment.—Biological literature has always taken account of what has been called "adaptation," or the *fitness of living things* for life in the surroundings or environment where they are placed. But a recent writer,[1] has elaborated the complimentary notion of *the fitness of the environment*. Recognizing living things as "mechanisms which must be complex, highly regulated, and provided with suitable matter and energy as food," he shows that the present inorganic environment is the best conceivable. Inorganic evolution has resulted, among other things, in the occurrence of large quantities of water and carbon dioxide; their physical and chemical properties, and those of the ocean, together with the chemical properties of the elements, carbon, oxygen, and hydrogen, and their numerous compounds, "are in character or in magnitude either unique or nearly so, and are in their effect favorable" to the organisms with which we are familiar, and which possess the three fundamental characteristics of complexity, regulation, and metabolism. The elements carbon, hydrogen, and oxygen, says Henderson, are uniquely and most highly fitted to be the stuff of which life is formed, and of the environment in which it exists.

73. Organic Evolution.—Developmental changes in living things constitute organic evolution. Such changes are manifested in the development of an individual from a spore or an egg. The development of a mature individual is *ontogeny*. The development of a group of related forms (genera, families, orders, etc.) is *phylogeny*. The chief problem of biology is to ascertain and record, in order, the evolutionary changes that have resulted in

[1] Henderson, Lawrence J. The fitness of the environment. New York, 1913.

the appearance of life and the present condition of living things.

The major problem of botany is to record, in order, the evolutionary steps that have culminated in the present condition of the plant world.

Organic evolution means that, after the first appearance of life, all living things, plant or animal, have been derived from preëxisting living things, in other words, that the present method of formation of living things, by the reproduction of organisms already existing, has always been the method—"*Omne vivum ex ovo*" (all life from an egg), "*omne vivum e vivo*" (all life from preëxisting life).

74. Method of Evolution.—To recognize that evolution is the method of creation still leaves unanswered the important question as to the method of evolution. By what process was the gradual development of the living world accomplished? Various hypotheses have been elaborated in answer to this question. We can here only briefly outline three of the most important ones.

1. *Agassiz's Hypothesis.*—The great teacher and student of nature, Louis Agassiz, believed that the vast array of plant and animal species, past and present, had no material connection, but only a mental one; that is, they merely reflected the succession of ideas as they developed in the mind of the Creator, but were not genetically related to each other. "We must . . . look to some cause outside of Nature, corresponding in kind to the intelligence of man, though so different in degree, for all the phenomena connected with the existence of animals in their wild state. . . . Breeds among animals are the work of man: Species were created by God."[1]

[1] Agassiz, L. "Methods of Study in Natural History," Boston, 1893, pp. 146, 147.

But to state that species were created by God does not satisfy the legitimate curiosity of the scientific man. What he wishes to know is: *By what method* was creation accomplished? God might have worked in various ways. Now, the study of Nature has never revealed to us but one method by which living things originate, and that is *by descent from preëxisting parents*. Agassiz's hypothesis

FIG. 45.—Louis Agassiz. (From Ballard's "Three Kingdom.")

contradicts this. All oaks now-a-days are derived by descent from preëxisting oaks, but the first oak, according to the doctrine of special creation, was created by supernatural means; it had no ancestors. The chief objection to the acceptance of this hypothesis is that the more profoundly and accurately we study living things, the more obvious it becomes that truth lies in another direction.

2. *Lamarck's Hypothesis.*—The noted French naturalist, Lamarck, taught that all living things have been derived from preëxisting forms; that the effects of use and disuse caused changes in bodily structure; that these changes were inherited and accentuated from generation to generation; that, being of use, those individuals possessing the changes in greatest perfection survived, while others perished; and that the derivation of new species is thus accounted for in a simple and logical manner. By continual reaching for tender leaves on high branches, the long neck of the giraffe was gradually produced, the slight gain in length in one generation being transmitted by inheritance to the next, and so on.

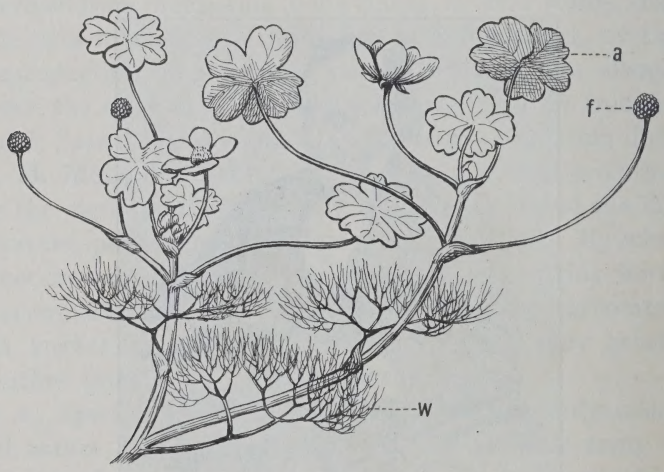


FIG. 46.—Water buttercup (*Ranunculus aquatilis*), showing aerial leaves (*a*), and aquatic leaves (*w*). *f*, fruit. Drawn from herbarium specimen.

The main thesis of Lamarck, as stated by himself, is as follows:

"In animals and plants, whenever the conditions of habitat, exposure, climate, nutrition, mode of life, *et cetera*, are modified, the characters of size, shape, relations between parts, coloration, consistency, and, in animals, agility and industry, are modified proportionately."

As illustrating the direct effect of environment on organisms, Lamarck chose a plant, the water-buttercup (*Ranunculus aquatilis*), which may grow in marshy places, or immersed in water (Fig. 46). When immersed, the leaves are all finely divided, but when not immersed, they are merely lobed.

While plants are more passive, and are affected by their surroundings directly, through changes in nutrition, light, gravity, and so on, animals react to environmental changes in a more positive and less passive manner. Thus, in the words of Lamarck:[1]

"Important changes in conditions bring about important changes in the animals' needs, and changes in their needs bring about changes in their actions. If the new needs become constant or durable, the animals acquire new habits. . . . Whenever new conditions, becoming constant, impart new habits to a race of animals . . . these habitual actions lead to the use of a certain part in preference to another, or to the total disuse of a part which is now useless. . . . The lack of use of an organ, made constant by acquired habits, weakens it gradually until it degenerates or even disappears entirely." Thus, "it is part of the plan of organization of reptiles, as well as of other vertebrates, that they have four legs attached to their skeleton . . . but snakes acquired the habit of glid-

[1] Translated from his *Philosophie Zoologique*, vol. I, pp. 227, 223, 224, 248.

ing over the ground and concealing themselves in the grass; owing to their repeated efforts to elongate themselves, in order to pass through narrow spaces, their bodies have acquired a considerable length, not commensurate with their width. Under the circumstances, legs would serve no purpose and, consequently, would not be used, long legs would interfere with the snakes' desire for gliding, and short ones could not move their bodies, for they can only have four of them. Continued lack of use of the legs in snakes caused them to disappear, although they were really included in the plan of organization of those animals."

On the other hand, "the frequent use of an organ, made constant by habit, increases the faculties of that organ, develops it and causes it to acquire a size and strength it does not possess in animals which exercise less. A bird, driven through want to water, to find the prey on which it feeds, will separate its toes whenever it strikes the water or wishes to displace itself on its surface. The skin uniting the bases of the toes acquires, through the repeated separating of the toes, the habit of stretching; and in this way the broad membrane between the toes of ducks and geese has acquired the appearance we observe to-day."

If such modifications are acquired by both sexes they are transmitted by heredity from generation to generation. This hypothesis is known as "the inheritance of acquired characters."

One of the weaknesses in Lamarck's hypothesis appears in his illustration of the snake. If we should grant that inheritance of the effects of disuse of the legs might possibly explain their absence in snakes, still it would not explain the *origin* of the snake's *desire to glide*. That is, of

course, as much a characteristic of the snake as the absence of legs.

Other arguments against the validity of Lamarckism are: first, that no one has ever been able to prove, by experiment or otherwise, that the effects of use (the so-called

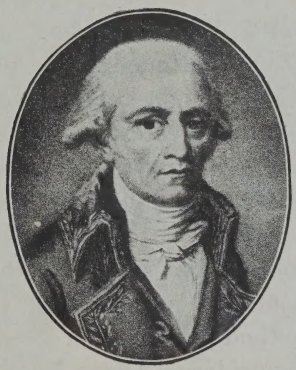


FIG. 47.—Jean Baptiste Lamarck (1744–1829). He elaborated the hypothesis of organic evolution by inheritance of the effects of use and disuse.

"acquired characters") are inheritable, while innumerable facts indicate that they are not; second, the hypothesis could apply only to the animal kingdom, since plants in general have no nervous and muscular activities like those of animals. A hypothesis of organic evolution, to be valid, must apply equally to both plants and animals.

3. *Darwin's Hypothesis.*—This will be outlined in the next chapter.

CHAPTER VII

DARWINISM

75. Darwin and Wallace.—The question of the method of evolution continued to be debated, with no satisfactory solution in sight, until 1859,[1] when Charles Darwin published the greatest book of the nineteenth century, and one of the greatest in the world's history, the *Origin of Species*.[2] This book was the result of over 20 years of careful observation and thought. It consisted of the elaboration of two principal theories: (1) that evolution is the method of creation; (2) that natural selection is the method of evolution.

By a strange coincidence Alfred Russell Wallace, also by many years of thoughtful observation, reading, and reflection, had independently formulated the conception of natural selection in far-off Ternate, and embodied his ideas in a paper which he sent to Darwin for the purpose of having it read before the Royal Society. The paper, with its accompanying letter, reached Darwin on June 18, 1858, while the latter was engaged in writing out his own views on a scale three or four times as extensive as that afterward followed in the *Origin of Species*. As a result of the unsurpassed magnanimity of the two men, and their generous attitude toward each other, it was

[1] This date should be memorized. It is one of the most important in the whole history of human thought.

[2] The full title of the book was "The Origin of Species by Natural Selection, or the Preservation of Favored Races in the Struggle for Life."

arranged to have a joint paper by Darwin and Wallace presented to the Society. This paper, entitled "*On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection*," was presented at a special meeting of the Society

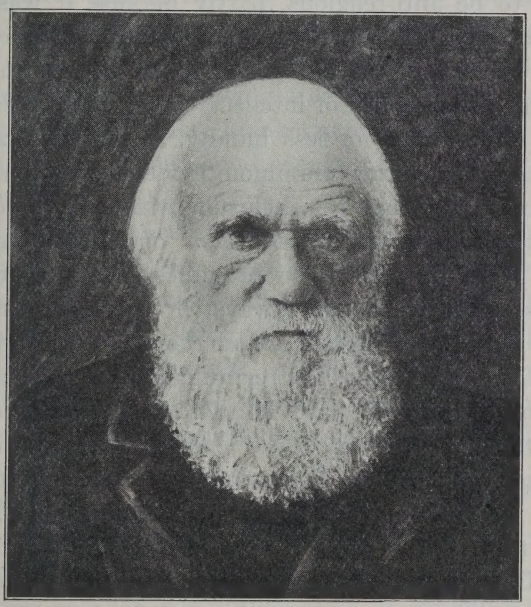


FIG. 48.—Charles Darwin. The publication of his "*Origin of Species*," in 1859, revolutionized human thought, and gave direction to all scientific and philosophic thinking from that time to the present.

on July 1, 1858, being read by the secretary in the absence of both Darwin and (of course) Wallace.

76. Early Antagonism to Evolution.—The conception that evolution (as distinguished from periodic, *supernatural* interventions of the Deity) is the method of

creation was arrived at independently by Darwin, but was not new with him. As we have just seen, it was proposed by Lamarck. Greek philosophers 2,000 years previously had suggested the idea; but it had never won the general acceptance of the educated world, partly because it was feared to be anti-religious, partly because it was never substantiated by sufficiently convincing evidence, and partly because of the antagonism of a few men of great influence in the world of intellect. Men preferred to follow a leader, more or less blindly, rather than take the pains to examine the voluminous evidence for themselves, and accept the logical conclusion without prejudice or fear, wherever it might lead them, or however much it might contradict all their prejudice and preconceived notions. But truth will always, in the end, command recognition and acceptance, and there is now almost no scientific man who does not regard evolution as axiomatic. It is one of the most basic of all conceptions, not only in the natural and the physical sciences, but also in history, sociology, philosophy, and religion; it has, indeed completely revolutionized every department of human thought.

77. Darwinism.—It is the second of the above mentioned theories, *i.e.*, natural selection, that constitutes the essence of Darwinism. The theory is based upon five fundamental facts, which are matters of observation, and may be verified by anyone, as follows:

1. *Inheritance.*—Characteristics possessed by parents tend to reappear in the next or in succeeding generations. We are all familiar with the fact that children commonly resemble one or both parents, or a grandparent or great grandparent, in some characteristic. From this we infer

that something has been inherited from the ancestor which causes resemblance in one or more characters—physical or mental.

2. *Variation.*—But the expression of the inheritance is seldom, if ever, perfect. Eyes are a little less or a little more brown; stature is never just the same; one-half the face may resemble a given ancestor more than another; petals may be *more or less* red or blue; no two oranges taste exactly alike; no two maple leaves are of precisely the same shape. There is inheritance, but inheritance is usually expressed with modifications or variations of the ancestral type.

3. *Fitness for Environment.*—It is common knowledge that living things must be adjusted to their environment. Poor adjustment means sickness or weakness; complete or nearly complete lack of adjustment means death. Water-lilies, for example, cannot live in the desert, cacti cannot live in salt marshes; cocoanuts cannot be grown except in subtropical or tropical climates, edelweiss will not grow in the tropics. This is because these various kinds of plants are so organized that they cannot adjust themselves to external conditions, beyond certain more or less definite limits or extremes. A cactus is fit to live in the desert because it is protected by its structure against excessive loss of water, and has special provision for storing up water that may be used in time of drought. Deciduous trees are fitted to live in temperate regions, partly because their deciduous habit and their formation of scaly buds enables them to withstand the drought of winter. Negroes live without discomfort under the tropical sun because they are protected by the black pigment in their skin. And so, in countless ways, we might illus-

trate the fact that all living things, in order to flourish, must be adjusted to their surroundings.

4. *Struggle for Existence.*—The clue to the method of evolution first dawned upon Darwin in 1838, while reading Malthus on "Population." Malthus emphasized the fact that the number of human beings in the world increased in geometrical ratio (by multiplication), while the food supply increased much less rapidly by arithmetical ratio (by addition). Therefore, argued Malthus, the time will soon be reached when there will not be food enough for all; men will then struggle for actual existence, and only the fittest (*i.e.*, the strongest, the fleetest, the most clever or cunning) will survive. In pondering this hypothesis Darwin at once saw its larger application.[1] There are always more progeny produced by a plant or an animal than there is room and food for, should they all survive. Darwin showed that the descendants of a single pair of elephants (one of the slowest breeders of all animals) would, if all that were born survived, reach the enormous number of 19,000,000 in from 740 to 750 years.[2] But the total number of elephants in the world does not appreciably increase: evidently many must perish for every one that lives.

[1] "In October 1838," says Darwin, "that is, 15 months after I had begun my systematic inquiry, I happened to read for amusement 'Malthus on Population,' and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favorable variations would tend to be preserved, and unfavorable ones to be destroyed. The result of this would be the formation of new species. Here then I had at last got a theory by which to work."

[2] One pair of elephants produces an average of only one baby elephant in 10 years, and the breeding period is confined to from about the 30th to the 90th year.

Linnæus, a century before Darwin, had called attention to the fact that if an annual plant produced only two seeds a year, and each of the plants from these seeds, in turn, produced two seeds the second year, and so on, there would, if all the individuals lived, be a million plants at the end of twenty years. But, few species breed as slowly as that. According to Kerner, the common broad-leaved plantain (*Plantago major*) produces 14,000 seeds annually; shepherd's purse (*Capsella Bursa-pastoris*), 64,000; and tobacco, 360,000. The number of seeds produced each year by the orchid, *Acropera*, was carefully estimated by Darwin at 74,000,000. But these figures are wholly surpassed by the ferns. Professor Bower estimates the number of spores produced each year by a well grown specimen of the shield fern (*Nephrodium filix-mas*) at from 50,000,000 to 100,000,000, while the estimate for the fern *Angiopteris* has been placed at 4,000,000,000 spores for a single leaf. One plant may have as many as 50 or more spore-bearing leaves. It has been pointed out that, at these rates of increase, unrestricted, a given species of plant would, in two or three years, cover an area several thousand times that of the dry land. But nothing of the sort occurs. There must, therefore, be an intense *struggle for existence*, in which the vast majority of individuals perish. Darwin[1] gives the following illustration:

"Seedlings, also, are destroyed in vast numbers by various enemies; for instance, on a piece of ground 3 feet long and 2 wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of 357 no less than 295 were destroyed, chiefly by slugs and

[1] "Origin of Species" (New York, 1902 edition), pp. 83, 84.

insects. If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the more vigorous plants gradually kill the less vigorous, though fully grown plants; thus out of 20 species growing on a little plot of mown turf (3 feet by 4) nine species perished, from the other species being allowed to grow up freely."

"*Struggle for Existence" Used in a Large Sense.*—"I should premise," said Darwin, "that I use this term in a large and metaphorical sense including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals, in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which only one on an average comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The mistletoe is dependent on the apple and a few other trees,[1] but can only in a far-fetched sense be said to struggle with these trees, for, if too many of these parasites grow on the same tree, it languishes and dies. But several seedling mistletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the mistletoe is disseminated by birds, its existence depends on them; and it may metamorphically be said to struggle

[1] In the above quotation, Darwin is undoubtedly referring to the European mistletoe (*Viscum album*). The American mistletoe (*Phoradendron flavescens*) is found in the eastern and central United States on various deciduous-leaved trees, including the sour gum and red maple.

with other fruit-bearing plants, in tempting the birds to devour and thus disseminate its seeds. In these several senses, which pass into each other, I use for convenience sake the general term of Struggle for Existence."

5. *Survival of the Fittest.*—In this struggle for existence only those best suited to their environment will survive. The dandelion from the seed that germinates first secures the best light; the one that sends down the longest and most vigorous root-system, that produces the largest, most rapidly growing leaves will survive, and will tend to transmit its vigorous qualities to its progeny. Less vigorous or less "fit" individuals perish. To this phenomenon Herbert Spencer applied the phrase, "survival of the fittest." Darwin called it "natural selection," because it was analogous to the artificial selection of favored types by breeders of plants and animals. It will be readily seen, however, that the process in nature is not so much a selection of the fittest, as a *rejection* of the unfit; the unfit are eliminated, while the fit survive. It has been suggested that "natural rejection" would be a better name than "natural selection." "Variations neither useful nor injurious," said Darwin, "would not be affected by natural selection."

78. Difficulties and Objections.—The publication of Darwin's "Origin of Species" aroused at once a storm of opposition. Theologians opposed the theory because they thought it eliminated God. Especially bitter antagonism was aroused by Darwin's suggestion that, by means of his theory "much light will be thrown on the origin of man and his history." The unthinking and the careless thinkers accused Darwin of teaching that man is descended from monkeys. Neither of these accusations, however,

is true. Darwinism neither eliminates God, nor does it teach that monkeys were the ancestors of men.

By slow degrees, however, men began to give more careful and unprejudiced attention to the new theory, and not to pass adverse judgment upon it until they were sure they understood it. "A celebrated author and divine has written to me," says Darwin, "that he has gradually learnt to see that it is just as noble a conception of the Deity to believe that He created a few original forms capable of self-development into other and needful forms, as to believe that He required a fresh act of creation to supply the voids caused by the action of His laws."

And in closing his epoch-making book, Darwin called attention to the fact that, in the light of evolution, all phases of natural science possess more interest and more grandeur.

"When we no longer look at an organic being as a savage looks at a ship, as something wholly beyond his comprehension; when we regard every production of nature as one which has had a long history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, in the same way as any great mechanical invention is the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting—I speak from experience—does the study of natural history become!"

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each

other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers having been orginally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved."

79. Objections from Scientists.—Objections to Darwin's theory were also brought forward by scientific men—partly from prejudice, but chiefly because they demanded (and rightly) more evidence, especially on certain points which seemed at variance with the theory. For example, they said, no one has ever observed a new species develop from another; this ought to be possible if evolution by natural selection is now in progress. The absence of "connecting links," or transitional forms between two related species was noted; the presence of apparently useless characters (of which there are plenty in both animals and plants) was not accounted for; and the geologists and astronomers claimed that the time required

for evolution to produce the organic world as we now behold it is longer than the age of the earth as understood from geological and astronomical evidence.

There is not space here to summarize the answers to all these objections. Suffice it to say that scientific investigation since Darwin's time has given us reasonably satisfactory answers to most of them, so that now practically no scientific man doubts the essential truth of evolution; it is the corner stone of all recent science, the foundation of all modern thought.

80. The Modern Problem.—But Darwinism left us with a very large and very fundamental problem unsolved. Upon what materials does natural selection act in the formation of species? Obviously the "fittest" survives, but *what is the origin of the fittest*? This problem Darwinism did not solve. The solution of it is one of the most fundamental and important tasks now being undertaken by biologists. The most effective attack is by the method of *experimental evolution*, which forms the subject of the next chapter.

CHAPTER VIII

EXPERIMENTAL EVOLUTION

81. A New Method of Study.—Previous to Darwin's time the study of plants and animals, was carried on chiefly by observations in the field. The science was largely descriptive—a record of what men had observed under conditions over which they did not endeavor to exercise any control; it was accurately named "Natural History" —a description of Nature. But Darwin and a few of his contemporaries, especially among botanists, began to make observations under conditions which they determined and largely regulated. In this way the problems were simplified, observation became more accurate, and the endeavor was made to assign the probable *causes* of the observed phenomena. With the introduction of this experimental method, science began to make rapid strides, and, more than ever before, facts began to be, not only recorded, but interpreted and explained.

82. Hugo de Vries.—The director of the Botanic Garden in Amsterdam, Holland, Hugo de Vries, was among the first to demonstrate that the method of experiment may be applied to the study of the origin of species. His plan was to secure seed of a given species from a plant which he believed to be *pure* with reference to a given character, that is, not contaminated or mixed by being cross-pollinated with another variety or species. The

characters of the parent plant were carefully noted and recorded by photographs and written descriptions, and by preserving dried and pressed herbarium specimens. The plants of the second generation were carefully guarded from being cross-pollinated, and thus "pure" seed were secured for a third generation. This was continued often for 25 or 30 generations of the plant, requiring as many

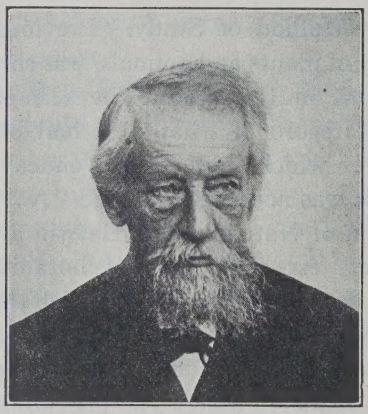


FIG. 49.—Hugo de Vries. His pioneer studies of osmosis resulted in fundamental contributions to our knowledge of that subject; his mutation-theory is one of the most important contributions to the study of evolution since Darwin.

years when a species produced only one crop of seed a year. Very careful records and preserved specimens were kept of the plants of each generation, and accurate comparisons were made to see if any individuals showed a tendency to vary widely from their parents in any significant way, such as showing entirely new characters, not expressed in the parents, or failing to manifest one or more of the characters of the parent.

83. Two Kinds of Variation.—One of the first results of de Vries's painstaking work was the demonstration of what he believed to be a fundamental difference between two distinct kinds of variation—*continuous* (or fluctuating) and *discontinuous* (or saltative, *i.e.*, leaping).

84. Continuous Variation.—Continuous variation is *quantitative*—a case merely of more or less. It deals with *averages*. Some flowers on a red-flowered plant may be lighter or darker red, but, in a series of generations, the

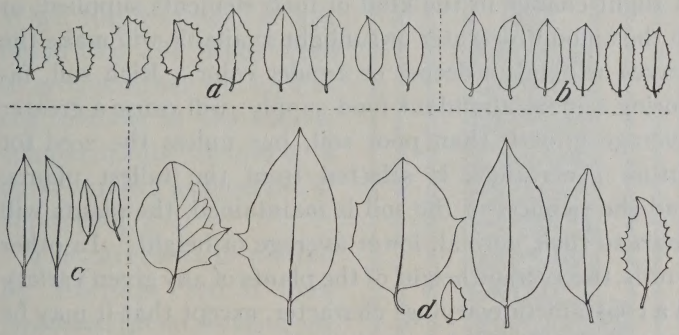


FIG. 50.—Fluctuating variation in the leaves of an oak (*Quercus chrysolepis*), *a*, all the leaves of a twig; *b*, younger leaves of a twig; *c*, consecutive leaves; *d*, some leaves on one season's growth of a twig. (After Copeland.)

average of a large number in each generation does not vary, and the departure from the average never exceeds certain limits. The flowers of a given species may have a certain characteristic odor, but the odor may be stronger in some flowers than in others, or in some individual plants than in others. The plants grown from a handful of beans of the same variety may vary in height *within limits*, but the *average* height of a large number will not vary in successive generations, and will be characteristic

of the species or variety. In other words, *continuous or fluctuating variation is variation about a mean.* It may be illustrated by the bob of a swinging pendulum, which continually fluctuates within definite limits about the mean position assumed when the pendulum is at rest (Fig. 56).

All plants and animals manifest fluctuating variation in all their characters (Fig. 50), and such variations are largely, if not entirely, dependent upon the environment. A slight change in the kind of food elements supplied, or in the amount of water or sunlight available will make the leaves or petals a deeper or a paler color. Rich soil, favoring a more abundant food supply, will cause a greater average growth than poor soil, but unless the seed for future generations is selected from the tallest plants, and the richness of the soil is maintained, the plants will *revert* to their normal, lower average of height. In other words, the average height of the plants of any given variety is a constant (unvarying) character, except that it may be *temporarily* altered by careful selection of seeds from the tallest or shortest individuals, or by choosing the largest or the smallest seeds from any given plant, or by making the soil richer or poorer, or otherwise. When the selection ceases, and the soil is maintained at average fertility, the characteristic *average* height of the plants is restored.

85. Illustrations of Continuous Variation.—In a quart of beans, for example, there are no two seeds of precisely the same proportion or size; some are longer, some shorter. De Vries describes[1] an experiment in which about 450 beans were chosen from a quantity purchased in the market, and the lengths of the indi-

[1] De Vries. "The Mutation Theory," vol. 2, p. 47, Chicago, 1909.

viduals measured. The length varied from 8 to 16 millimeters, and in the following proportions:

Millimeters.....	8	9	10	11	12	13	14	15	16
Number of beans.	1	2	23	108	167	106	33	7	1

The beans were then placed in a glass jar divided into nine compartments, all the beans of the same length in the same compartments. When this was done it was found that the beans were so grouped that the tops of the columns in the various compartments followed a curve, known as Quételet's[1] curve (Fig. 51).

This curve may be plotted by erecting vertical lines (*ordinates*) at intervals of one millimeter on a horizontal line or base, the height of each vertical line being proportionate to the *number* of beans having the length indicated in figures at its base. This curve shows the *frequency* of occurrence of seeds of any given dimension

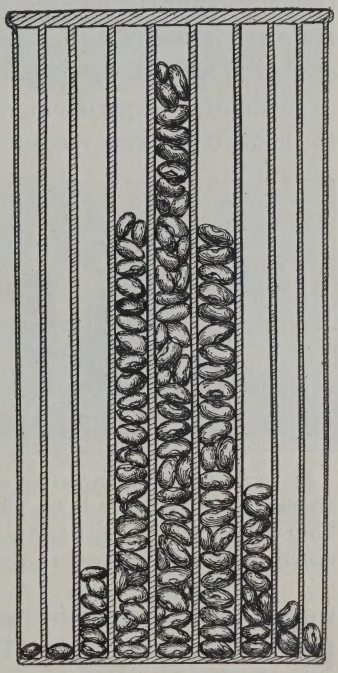


FIG. 51.—Demonstration of Quételet's law of fluctuating variability in the length of seeds of the common bean (*Phaseolus vulgaris*). Description in the text. (Redrawn from de Vries.)

[1] So named from its discoverer, Quételet (Ket-lay). As de Vries states: "For a more exact demonstration a correction would be necessary, since obviously the larger beans fill up their compartment more than a similar number of small ones."

between the two limits or extremes, and is therefore often referred to as a *curve of frequency*. It should be noted that, in the case illustrated, the greatest frequency (indicated by the highest point of the curve) very nearly coincides with the *average* dimension; in other words, *the more any given character departs from the average for that character, the less frequent is its occurrence.*

In another experiment, ears of corn, harvested from the same crop, were measured and found to vary in length

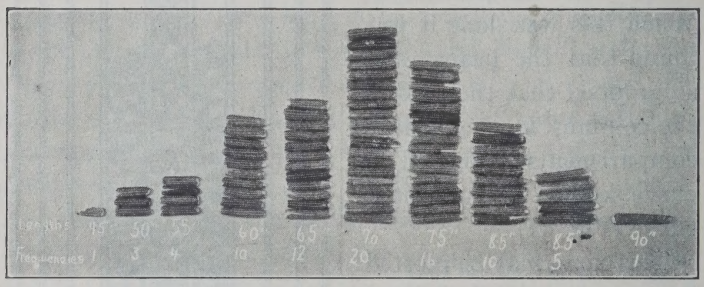


FIG. 52.—Curve of fluctuating variation (Quételet's curve), formed by arranging 82 ears of corn in ten piles, according to the length of the ears. The extremes were 4.5 and 9 inches. The ears were taken from unselected material from a field of corn. (After Blakeslee.)

from 4½ inches to 9 inches; the largest number of ears (20) were 7 inches long. The greater the departure from this length, in either direction, the fewer the individuals; for the lengths 4 inches and 9 inches the frequency was zero. When the ears were arranged in piles according to their length, the tops of the piles indicated the curve of frequency (Fig. 52).

The curve of frequency indicates the quantitative distribution of any character or quality when its occurrence is dependent largely upon chance. This is strikingly

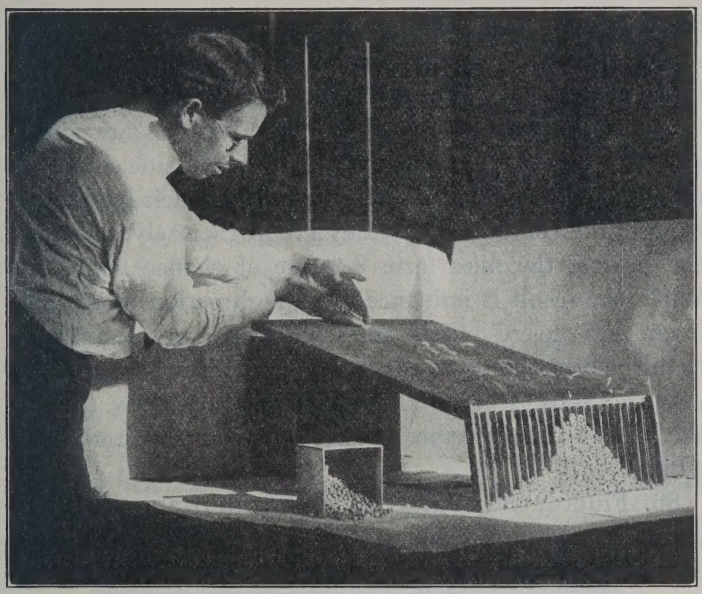


FIG. 53.—Photograph of beans rolling down an inclined plane and accumulating at the base in compartments, which are closed in front by glass. The exposure was long enough to cause the moving beans to appear as caterpillar-like objects hopping along the board. If we assume that the irregularity of shape of the beans is such that each may make jumps either toward the right or toward the left in rolling down the board, the laws of chance lead us to expect that in very few cases will these jumps be all in the same direction, as indicated by the few beans collected in the compartments at the extreme right and left. Rather the beans will tend to jump in both right and left directions, the most probable condition being that in which the beans make an equal number of jumps to the right and to the left, as shown by the large number accumulated in the central compartment. If the board be tilted to one side, the curve of beans would be altered by this one-sided influence. In like fashion, a series of factors—either of environment or of heredity—if acting equally in both favorable and unfavorable directions, will cause a collection of ears of corn to assume a similar variability curve, when classified according to their relative size. Such curves, called Quételet's curves, are used by biometricians in classifying and studying variations in plants and animals. (Photo by A. F. Blakeslee. Legend slightly modified from Journal of Heredity, June, 1916.)

illustrated by the grouping of bean seeds rolled down a smooth inclined plane, and collected in receptacles at the bottom (Fig. 53). The seeds are started rolling midway between the edges of the plane; the chances are about equal for some of the seeds to fall into the outside compartments, but the odds are vastly in favor of their landing at or near the center. Thus they group themselves so that the tops of the piles form a curve of chance variation. When the result is influenced in one direction more than in another the crest of the curve will be nearer one extreme than the other, and the curve is to that extent *skew*. The curve of bean seeds in Fig. 53 is slightly skew toward the right-hand extreme. Suggest one or more reasons why.

86. Fluctuating Variation and Inheritance.—When the ancestry is not mixed or hybrid the curve of frequency of any character in one generation ordinarily tends to recur in successive generations of descendants, providing the environment remains essentially the same.[1]

87. Discontinuous Variation.—Long before Darwin, students of plants and animals had observed a different kind of variation than continuous—one which was not quantitative but *qualitative*, resulting in the expression of new characters, or of a *new curve of frequency*; that is, in fluctuation about a new mean. Plants from *some* of the seeds of a red-flowered specimen bear flowers, not that vary from deeper to paler red, but that suddenly, at one step, have become pure white; one or more seeds from an odorless plant may give rise to individuals whose flowers are sweet-scented; or *vice versa*, odorless specimens

[1] The behavior of hybrid descendants is a special case described in Chapter XXXVII.

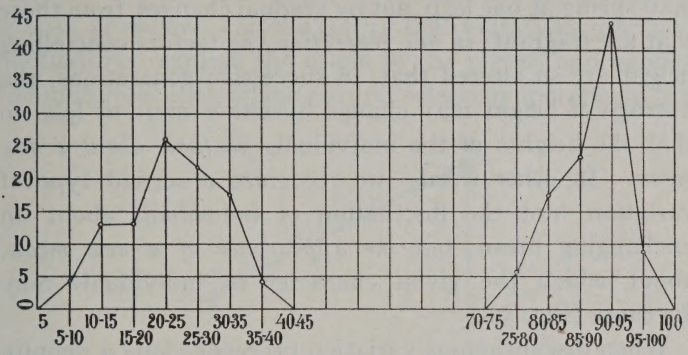


FIG. 54.—Curves of variation, illustrating the difference between fluctuation about a given mean, and the appearance of a new mean, *i.e.*, mutation. At the right, variations in the stature of *Oenothera Lamarckiana;* at the left, variation in the stature of *Oenothera nanella,* a form derived from *O. Lamarckiana* by mutation. (After de Vries.)

FIG. 55.—Leaves of varieties of the Boston fern (*Nephrolepis*), showing (from left to right) progressive branching of the pinnæ and pinnules, and illustrating so-called "orthogenetic saltation." (After R. C. Benedict.)

may spring at one leap, not by gradual changes, from those that are fragrant; *in one generation* the factors controlling height are so altered that, in successive generations, the average of height may change by either more or less, so that the heights of the individuals *fluctuate about a new mean.* In other words, we recognize a second type of variation—not the fluctuation of *individuals* about an unchanging mean, but *the appearance of a new mean,* about which the given character in individuals may fluctuate (Fig. 54.)

When discontinuous variation proceeds along a definite line through several successive generations, each step being an intensification of the preceding one, it is designated "*orthogenetic saltation*" (Fig. 55).

88. Illustration of the Pendulum.—The difference between discontinuous and fluctuating variation may be aptly illustrated by a swinging pendulum (Fig. 56). The vertical position, assumed when at rest, is the mean of all positions that may be assumed as the pendulum swings; the oscillation about this mean illustrates continuous or fluctuating variation.

But we may conceive that the point of suspension of the pendulum changes, as shown in the figure. The pendulum continues to oscillate, but now about a new mean position; *a new character has been introduced,* with its own fluctuations of more or less.

89. Mutations.—Darwin, as well as others before and after him, recognized both kinds of variation, but de Vries was the first to work out in detail the hypothesis that *discontinuous variations furnish the material for natural selection.* Discontinuous variations he called *mutations;* plants which give rise to or "throw" them are said to

mutate. A plant that arises by mutation is an *elementary species*, or *mutant;* and the theory that mutations (and not fluctuations) explain the origin of the fittest, and supply the materials upon which natural selection operates in the

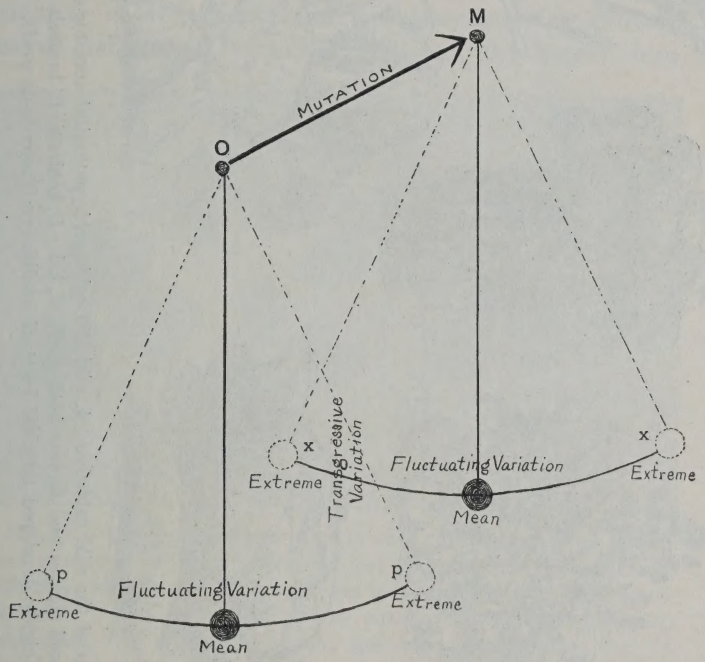


FIG. 56.—Diagram to illustrate the difference between fluctuating variation and mutation; *O*, original point of suspension; *M*, new point of suspension after the mutation has occurred.

formation of new species, de Vries called *the mutation theory.*

90. Examples of Mutation.—The kohlrabi, cauliflower, and other horticultural varieties of the wild cliff-cabbage (Fig. 57), are believed to be mutants, and to have arisen,

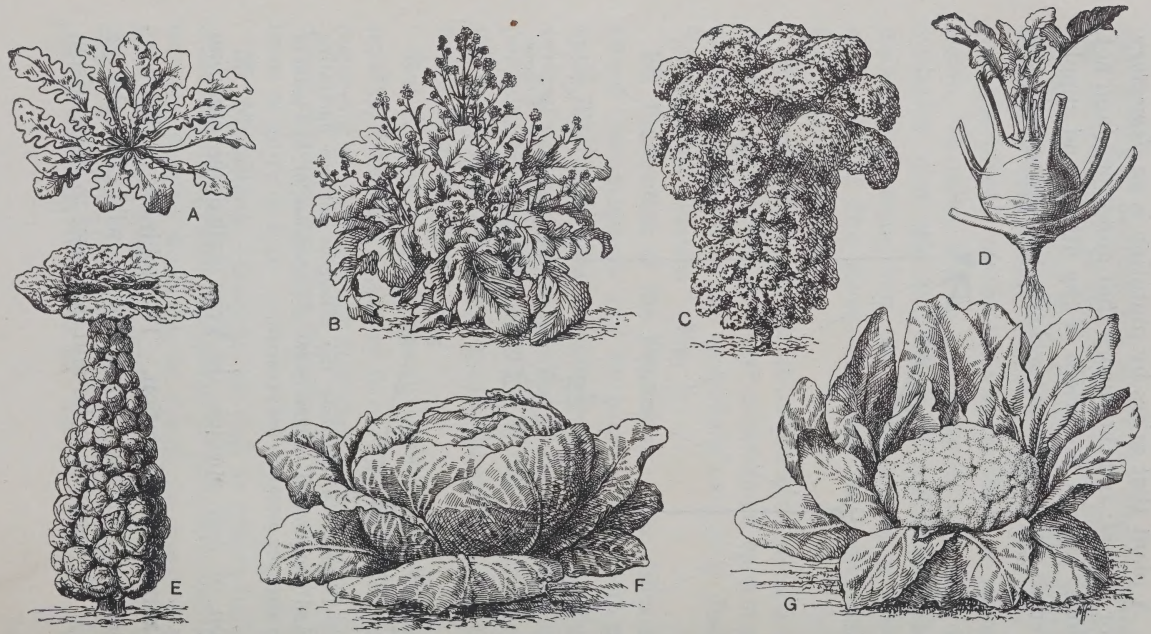


FIG. 57.—Horticultural varieties of the wild cabbage. *A*, wild cliff-cabbage, hypothetical ancestor of the numerous modern horticultural forms; *B*, broccoli (leaves and flowers both used); *C*, kale; *D*, kohlrabi; *E*, brussels sprouts (lateral buds used); *F*, common cabbage (a highly developed terminal bud); *G*, cauliflower (flower-buds used). (Redrawn from various sources.)

not by the prolonged selection of fluctuating variations, but at one step—in one generation—as "sports" of the wild *Brassica oleracea*. Strawberry plants without runners, green dahlias and green roses, the common seedless bananas of the markets, the Shirley poppies, pitcher-leaved ash trees, Pierson's variety of the Boston fern,

FIG. 58.—Clover leaves with three to nine leaflets, illustrating a tendency to mutate. The normal clover leaf is a pinnately compound leaf with three leaflets. Plants with leaves having five to nine leaflets constitute a "half-race," *i.e.* the normal character is active, the anomaly semi-latent. (Photo by the author; specimens from cultures of G. H. Shull.)

5–9- "leaved" clovers (Fig. 58), white black-birds (and other albinos, including albino men), moss-roses, thornless cacti and thornless honey-locusts, red sunflowers, composites with tubular corollas in the ray-flowers (Fig. 48), and the innumerable white flowered varieties of colored flowered species, are all illustrations of mutation. Frequently the mutative change occurs in a lateral bud, pro-

ducing a "bud-sport" (Fig. 60). Such was the origin of the seedless naval orange from the seed-bearing orange.

91. The Evening-primrose.—In 1886 de Vries began to search for a species that was in a mutating condition, be-

FIG. 59.—Yellow daisy, or cone-flower (*Rudbeckia sp.*), showing variations of the character of mutations in the ray- and disc flowers. At *d* the normally ligulate corollas are tubular; at *f* they have all aborted, except two; at *h* many of the normally tubular disc-flowers have become ligulate, making a nearly "double flower." (Photo by E. M. Kittredge.)

lieving that any given species is at some periods in its history more labile or changeable than at other periods. After a long search he found, in an abandoned potato field at Hilversum, near Amsterdam, a large number of plants of Lamarck's evening-primrose (*Œnothera Lamarckiana*) (Fig. 61).

"That I really had hit upon a plant in a mutable period became evident from the discovery, which I made a year later, of two perfectly definite forms which were immediately recognizable as two new elementary species. One of them was a short-styled form: *O. brevistylis*, which at first seemed to be exclusively male, but later proved to have

FIG. 60.—A plant of the evening-primrose (*Œnothera biennis*) which, by "bud sporting," has given rise (at the left) to a branch having the characters of another species.

the power, at least in the case of several individuals, of developing small capsules with a few fertile seeds. The other was a smooth-leaved form with much prettier foliage than *O. Lamarckiana*, and remarkable for the fact that some of its petals are smaller than those of the parent type, and lack the emarginate form which gives the petals of

Lamarckiana their cordate character. I call this form *O. lævifolia.*"

"When I first discovered them (1887) they were represented by very few individuals. Moreover each form occupied a particular spot on the field. *O. brevistylis* occurred quite close to the base from which the *Œnothera*

FIG. 61.—Lamarck's evening-primrose (*Œnothera Lamarckiana*). A mutating species. *Cf.* Fig. 62. (After de Vries.)

had spread; *O. lævifolia* on the other hand, in a small group of 10 to 12 plants, some of which were flowering whilst others consisted only of radical leaves, in a part of the field which had not up to that time been occupied by *O. Lamarckiana.* The impression produced was that all these plants had come from the seeds of a single mutant.

Since that time, both the new forms have more or less spread over the field" (*de Vries*).

Another mutant of *O. Lamarckiana* was called by de Vries *Œnothera gigas* (Fig. 62). The cells of this mutant have twice as many chromosomes as the parent form.

FIG. 62.—Giant evening-primrose *Œnothera gigas*, a mutant from *Œnotheta Lamarckiana*, originated in 1895. *Cf.* Fig. 61. (After de Vries.)

92. The Test of a Mutation.—The deciding test as to whether a given new form, arising without crossing from a form that has bred true for at least two generations, is really a mutant or merely a fluctuating variant, is to see if it breeds true to seed for the new character or characters.

If it does it is a mutant; otherwise it is not. It is clear, therefore, that the only way the problem can be followed out is by experiment—hence the term *experimental evolution*. The next step for de Vries to take, after discovering the two forms that he supposed to be mutants, was to breed them in carefully guarded, pedigreed cultures in his garden, and also to breed the parent form, *Œnothera Lamarckiana*, and see if he could observe the two forms above mentioned, or other mutants, arise from seed produced without crossing with any other species.

The entire story of this classical series of experiments is too long to be told here. Suffice it to say that de Vries did observe numerous other aberrant forms arise, and also found that they bred true (except for additional mutations) when propagated by seed for over 25 years—that is, they were true mutations.

93. Relation of Mutation Theory to Darwinism.—The mutation theory is not intended by de Vries to supplant the theory of natural selection, but to demonstrate that the materials upon which selection acts *in the formation of new species* are mutations, and mutations only—never fluctuating or individual variations. Here lies the essential difference between Darwin and de Vries, for Darwin, though recognizing, and with increasing clearness, that mutation furnishes part of the material to be "selected" by nature, assigned a larger and more important rôle to fluctuating or individual variations. "Species have been modified," he said, "chiefly through the natural selection of numerous successive, slight, favorable variations; aided [however] in an important manner by . . . . variations which seem to us in our ignorance to arise spontaneously. It appears that I formerly underrated the frequency and

value of these latter forms of variation, as leading to permanent modifications of structure independently of natural selection.[1] And he goes on to say that, "as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work (the *Origin*), and subsequently, I placed in a most conspicuous position —namely, at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.'"[2]

In the second place, the mutation theory explains away numerous objections to natural selection. It shows how characters that are never of vital importance[3]—*i.e.*, matters of actual life or death—to a species may arise and be perpetuated. Without mutation this is difficult to explain,[4]

[1] Darwin, C. *The Origin of Species.* 6 Ed. New York. D. Appleton & Co., 1902, p. 293.

[2] Darwin almost dispaired of making his position on this point understood. The clear statement above quoted, he said, "has been of no avail. Great is the power of steady misrepresentation; but the history of science shows that fortunately this power does not long endure." Darwin. l. c., p. 293.

[3] As required by Darwin's theory. See quotation above (p. 118), and on p. 97.

[4] Other explanations have been offered. For example, sometimes two characters appear to be always associated, so that the presence of one involves the presence of the other; as a mane and maleness in the lion, dicotyledony and exogeny in Angiosperms. The constant association of two characters is often (though not always) due to the fact that the factors for those characters tend to keep together in the same chromosome, instead of segregating during the formation of egg-cells and sperms. This tendency is called *linkage.* The association of smooth (vs. wrinkled) seed with tendrilled (vs. non-tendrilled) leaves in the garden pea, and of red flower-color with round pollen in the sweet pea may be cited as examples of linkage. In such cases one of the characters might be of vital importance to a plant in the struggle for existence and the other not.

and yet many, if not most, of the characteristics by which different species are distinguished from each other are of this kind—not, so far as we can see, absolutely essential to the life of the species. Mutation also offers a method by which evolutionary changes may take place within a much shorter time-period than was demanded by the natural selection of fluctuations. Incidentally, the mutation theory clearly shows that the absence of "connecting links" between species is not, as was formerly urged, an argument against evolution, but is, on the contrary, just what we might expect to find.

94. Value of the Mutation Theory.—The elaboration of the mutation theory (together with the rediscovery of Mendel's law, to be discussed in Chapter V) furnished the biological world with a new method of study; it demonstrated that the method of evolution, so far as it concerns the origin of new characters, may be studied by experimentation.[1] The mutation theory should also be of great service to breeders. It has helped to establish plant and animal breeding on a more scientific basis, has pointed the way to correct methods where men where formerly groping in the dark, and has showed, that results of commercial value do not require a life time, but may be obtained within two or three seasons. By the application of modern methods it has been possible, within a few seasons, to

[1] Like most great contributions to science, the elaboration of the experimental method of approach to the problem of heredity and evolution cannot be attributed solely to any one man. Students of science in any period come into a rich inheritance in the labors of many predecessors. To fully assign the credit for the experimental method in the study of heredity it would be necessary to write the history of investigations extending from Kölreuter (1760) one of the first, if not the first hybridizer, of plants, Knight (1799), through Gaertner (1849), Jordan (1853), Naudin (1862), and others to Mendel, de Vries, and those of more recent date, down to our own time.

obtain new strains of oats yielding as much as 14 bushels per acre more than the variety from which they were derived, and to produce new strains of corn not only giving a larger yield, but maturing nearly two weeks earlier than the parent variety.

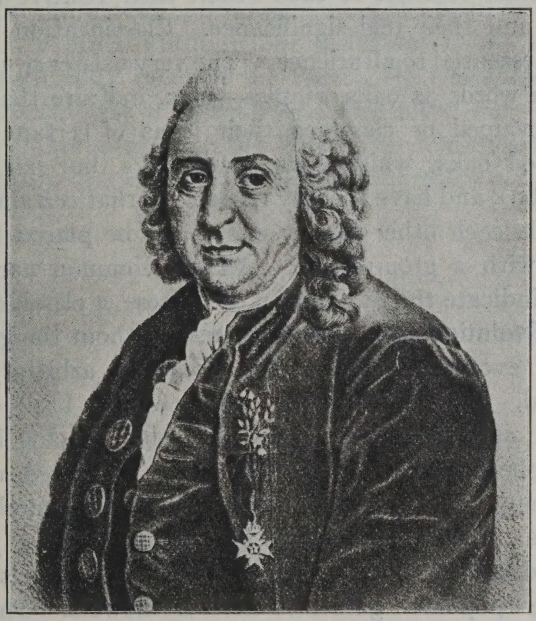


FIG. 63.—Linnæus, the great classifier (1707–1778). He is wearing a sprig of the twin-flower (*Linnæa borealis*), one of his favorite flowers, and named after him by his friend, Gronovius. He is regarded as the father of modern systematic botany.

95. Classification.—Mere information is not science. A "book of facts" is not a scientific treatise for it is composed of bits of unrelated information, presented on some artificial basis of sequence, as for example, alphabetically.

Scientific knowledge, in addition to being as accurate as possible, is characterized by having an orderly arrangement in one's mind, and this order is based on a logical, fundamental relationship between the facts and ideas. Only by such an arrangement of our ideas are we able to understand their relation to each other, their relative importance, and their real significance. Classification, therefore, is essential to all science. The very existence and use of such words as oaks, maples, roses, indicate that men have grouped or classified their ideas of certain plants (*e.g.*, red oaks, white oaks, black oaks, bur oaks, live oaks, etc.), and have thereby recognized that certain kinds resemble each other closely enough to be placed in one group with a group-name. All the common names of plants indicate the recognition of classes—a classification.

96. Evolution and Classification.—Without the guiding idea of evolution classification would be arbitrary and artificial. Linnæus classified plants on the basis of the number of stamens they possessed, thus placing in one group plants now known to be wholly unrelated, except that they have a chance similarity in the number of stamens. In like manner we may group together plants with red flowers, blue flowers, or pink flowers, as is often done in "popular" guides to the wild flowers. This has its value, but it tells us really nothing about the significant relationship between plants, does not help clear up our own ideas, does not show the gaps in our knowledge and tell us where to search for new facts to fill up the gaps. Evolution, by showing that plants are all related to each other by descent, just as are the members of a large family of persons, discloses to us the only true basis of classification—the plan that endeavors to arrange all plants so as to

show their descent and their relationship to each other. Without evolution there might be any number of arbitrary systems; on the basis of evolution there can, in the end, be but one true system, which all students must accept, because it will be a true record of what has actually occurred in the history of development of the plant or animal world. In other words, *if our knowledge should ever become sufficiently complete and exact, the classification of plants would give a summary—a bird's eye view—of the course of evolution and the history of development. To approximate this end is one of the largest problems of botany.*

CHAPTER IX

THE EVOLUTION OF PLANTS

97. The Problem Stated.—If we knew the entire history of development of the plant world, we could arrange all plants now living, and that have lived, so as to show their genetic relation to each other. The problem is illustrated on a small scale by various related cultivated plants, all known to be derived from a common wild ancestor. Cabbage and its relatives are a case in point. The botanical relatives of the cabbage include such forms as kohlrabi, brussels-sprouts, collards, kale, broccoli, and cauliflower (Fig. 44). All of these garden vegetables are believed to have been derived from the common wild cliff-cabbage (*Brassica oleracea*) of Europe and Asia, by selecting mutations in various directions, *e.g.*, excessive development of the stem in kohlrabi, of the terminal bud in cabbages, of the lateral buds in brussel's sprouts, of the flower buds in cauliflower. Or, to refer to de Vries's studies in experimental evolution, where the course of descent was actually observed, we may arrange the forms of Lamarck's evening-primrose so as to show their known derivation.

The general problem, therefore, is to establish the genetic relationship of all known plants, living and fossil. Since the Angiosperms stand at the top of the series, the problem resolves itself largely into ascertaining the *phylogeny*, or line of ancestry, of that group.

98. Methods of Study.—In the solution of this problem two methods of attack may be employed: (1) That of observation and comparison of structure, followed by classification, and inference; (2) that of experiment. The use of experiment is indicated in Chapters V and VIII. By this means we may learn something of the relationship of different groups having living representatives, but it chiefly serves to throw light on the *method* of evolution. The *course* of evolution is best ascertained by the observation and comparison of plant structures.

99. Sources of Evidence.—There are five main sources of evidence as to the course of evolution:

1. *Comparative life histories of living forms.*
2. *Comparative anatomy of living forms.*
3. *Geographical distribution.*
4. *Structure of fossil forms.*
5. *Geological succession of fossil forms.*

Studies along these five different lines have resulted in some conflict of evidence, but on the whole the evidence from the various sources all points to the same broad conclusions. Conflict or contradication is in most cases the result of insufficient evidence from one or more sources.

100. Evidence from Life Histories.—In the study of the life history (*ontogeny*) of any higher sporophyte, we find that vegetative (sterile) tissues develop first. On the basis of this fact it has been inferred by some investigators[1] that all reproductive organs (stamens, carpels, sporophylls) arose by a modification of vegetative organs. Other facts, however, as set forth on pages 126–129, have lead to the directly opposite conclusion.

[1]See Bower, F. O. "*The origin of a land flora.*" Macmillan and Co. Ltd., London, 1908.

101. Evidence from Comparative Ontogeny.—In zoology, evidence of the course of evolution is also seen in the *recapitulation* of the characters of lower forms in the embryogeny of higher forms. This is often referred to as von Baer's law. Evidence of that nature is less striking and less common in plants. It is found, however, in a comparison of the young or embryonic stage of the sporophyte of the higher liverwort, *Marchantia*, with the mature

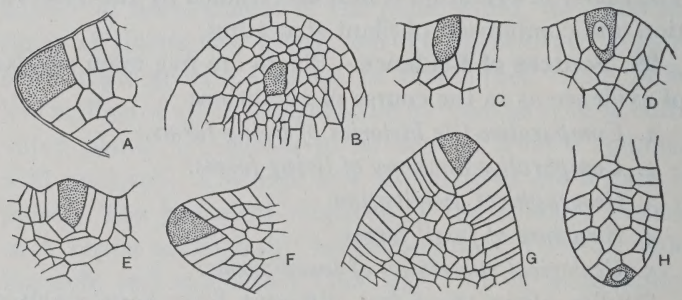


FIG. 64.—The apical cell in the stem apex in various phyla, from Bryophytes to Gymnosperms. *A*, acrogynous liverwort (*Notothylus orbicularis*); *B* & *C*, eusporangiate ferns (*B*, *Marattia Douglasii*, *C*, *Ophioglossum pendulum*); *D* & *E*, homosporous leptosporangiate ferns (*D*, *Osmunda Claytoniana*, *E*, *Adiantum emarginatum*, representing Polypodiales); *F*, heterosporous leptosporangiate fern (*Marsilia vestita*); *G*, a horsetail (Calamophyte) (*Equisetum telamateia*); *H*, a late gymnosperm (*Pinus Laricio*). (*A–G* redrawn from Campbell, *H* from Buchholz).

sporophyte of the lower liverwort *Riccia* (Fig. 65). The latter consists almost entirely of "fertile" (*i.e.*, reproductive) cells. As we pass to more highly organized forms, such as *Marchantia*, the relative amount of vegetative tissue gradually increases by a *progressive sterilization*[1] of fertile tissue. This progressive sterilization is repeated in the ontogeny of the sporophytes of the higher forms. The thread-like, green *protonema* of mosses is often in-

[1] See foot-note, p. 125.

terpreted as reminiscent of an ancestral filamentous green alga, and the appearance in the embryo of pines and other conifers of a larger number of primordia than of mature cotyledons, has also been regarded as a recapitulation of an ancestral feature (Fig. 104). Bucholz[1] has demonstrated that young pine embryos possess an apical cell similar to that characteristic of ferns and fern-allies, this apical cell persisting until the pine embryo comprises several hundred cells, and then loosing its identity (Fig. 64).

102. Evidence from Comparative Anatomy.—Comparative study of structure has led to the conclusion that, in its broadest aspects, the course of plant evolution has been from the simple to the complex; that such simple organisms as *Pleurococcus*, and other green algæ, preceded more complex forms like the liverworts; that Bryophytes probably appeared before ferns, and they in turn before the modern Gymnosperms and Angiosperms.

A difficulty of accepting this conclusion as final is the possibility that, at certain points, the course of evolution may have been retrograde—*i.e.*, from the more complex to the less complex. For example, it is generally accepted that the filamentous, alga-like fungi were derived from green algæ by retrograde evolution (degeneration). Were the plants with one seed-leaf (monocotyledons) derived from those with two (dicotyledons) by retrograde evolution, or were the dicotyledons derived from the monocotyledons by progressive evolution? Evidence ascertained by comparative studies of vascular anatomy and other details of structure points to the conclusion, that, although

[1]Bucholz, J. T. Suspensor and Early Embryo of *Pinus*. *Bot. Gaz.* 66: 185–228. Sept., 1918.

monocotyledony seems the simpler, more primitive condition, it is really a later phenomenon, the monocotyledons being derived from the dicotyledons by simplification.[1]

As a further example there may be cited the application of the method of comparative anatomy to solve the problem

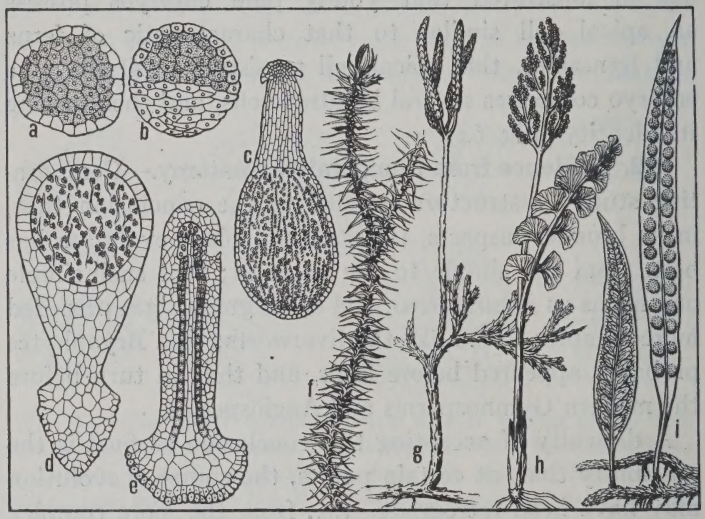


FIG. 65.—Progressive sterilization of tissue in sporophytes. *a*, *Riccia trichocarpa* (mature); *b*, *Marchantia polymorpha* (embryo); *c*, *Marchantia* (mature); *d*, *Porrella*, a leafy liverwort (mature); *e*, anthoceros; *f*, *Lycopodium Selago;* *g*, *Lycopodium complanatum;* *h*, *Botrychium Lunaria* (Eusporangiate); *i*, *Polypodium venosum* (Leptosporangiate). (Redrawn from various sources.)

of the origin of the leafy sporophyte. As noted above (¶101), the most primitive spore-producing phases (sporophytes) of the lower liverworts (Hepaticæ) consist almost entirely of "fertile" (*i.e.*, reproductive) cells, and the relative amount of vegetative or sterile tissue

[1] See page 223.

gradually increases, as we pass to more highly organized forms, indicating a progressive sterilization of the fertile tissue during evolutionary development. A survey of the sporophytic phases of the liverworts, mosses, and ferns will show how these sporophytes gradually increase in complexity and importance, from the simple condition in the liverwort *Riccia*, with almost no sterile tissue, through the sporogonium of the higher liverworts and mosses, to the leafy sporophyte of the ferns (Fig. 65). The final step in the development of the sporophyte was the differentiation of plants bearing only large spores (*megasporophytes*), and those bearing only small spores (*microsporophytes*), represented in the Angiosperms respectively by the pistillate and staminate plants. The progressive sterilization accompanied a change in the habitat of the plants from water to dry land.[1]

On the other hand, a careful student of fossil plants has recently been led to state that, "it is beginning to appear more probable that the Higher Cryptogams (ferns and fern allies) are a more ancient and primitive group than the Bryophytes, which would seem to owe their origin to reduction from some higher type."[2] In view of this diversity of opinion, we learn at once that great caution must be used in interpreting the evidence—that we must not "jump at conclusions."

103. Results of the Method of Comparative Anatomy. By their study of comparative anatomy and morphology, botanists have been led to propose the following

[1] "The fern, as we normally see it, is an organism with, so to speak, one foot in the water, the other on the land." Bower, F. O., *The origin of a land flora*. p. 82.

[2] Scott, D. H. *The Evolution of Plants*. p. 18.

arrangement of plant groups as representing *the general course* of their evolution (Table I):

From what has already been said, however, it should be understood that such a table represents, not the line of evolutionary advance, but the paths travelled by plants in the course of their development. For example, it implies that dicotyledons were derived from monocotyledons, pteridophytes from bryophytes—hypotheses which, from other trustworthy evidence, as stated above, now seem untenable.

TABLE I.—SEQUENCE OF PLANT GROUPS, BASED ON THE MORPHOLOGY OF LIVING FORMS

Thallophytes (no archegonia)	Algæ—having chlorophyll. Fungi—no chlorophyll.
Archegoniates (archegonia, but no seeds)	Bryophytes—no vascular system. Pteridophytes, Calamophytes, Lepidophytes } vascular system.
Spermatophytes (seeds)	Gymnosperms—no closed ovary. Angiosperms—closed ovary (pistil). Monocotyledons—one-seed leaf. Dicotyledons—two-seed leaves.

Again, the table suggests that Angiosperms were derived from Gymnosperms, and therefore appeared late in the history of plant life; but the study of fossil plants shows that they appeared in the geological past, and were dominant in the Tertiary period, as now, We are led, therefore to proceed with caution in drawing inferences based only upon a comparative study of the structure of forms now living.

104. Consequences of an Amphibious Habit of Life.—The life history of the fern affords a concrete illustration

of the consequences of a change from an aquatic to an amphibious habit of life. The gametophyte is semi-aquatic in habit, and the method of fertilization is purely aquatic, the sperm being unable to reach the egg except by swimming through free water.[1] But, when the fertilized egg began to develop as a land plant, the chances of fertilization by a sperm swimming in free water became increasingly remote. The perpetuation of the species, and the multiplication of individuals could be insured only by the formation of a large number of reproductive bodies (spores), capable of distribution by wind in dry conditions, and each able to reproduce its kind independently, without fusion with another reproductive body. The larger the number of such spores, the greater the chances of perpetuation of the given species.

105. Consequence of Enormous Spore-production.—But the formation of a large number of spores requires a vigorous plant body to supply them with an abundance of water and nourishment, and to lift them up into the air where they would stand a better chance of distribution when dry. This is accomplished by the sporophyte, producing an abundance of broad, green leaves for food-manufacture, and of roots for absorption of water and minerals in large quantities. From such considerations as these the plant body of the sporophyte is regarded by Bower and his followers as produced by the progressive sterilization of tissues originally reproductive. After the formation of a vigorous plant body, spores, produced in special regions (sporangia) could be nourished in enormous numbers.

106. Origin of Vegetative Organs.—On the basis of Bower's theory we are to regard foliage leaves and branches,

[1] See p. 23.

either as *new formations*, developed (by "*enation*") on some primitive reproductive axis like a strobilus or cone, or else

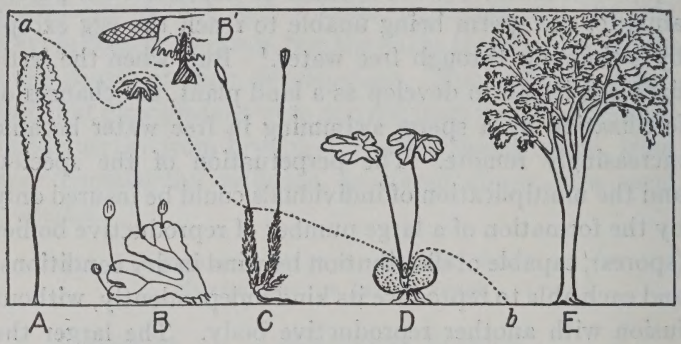


FIG. 66.—Diagram to show the increase in prominence of the sporophyte stage of plant life from the algæ to the higher seed-plants. Among the thallophytes both the sexual and asexual methods of reproduction are represented. *A* illustrates the asexual, wherein certain cells of the plant divide into smaller cells, the zoöspores, which, without union with other cells, develop directly into new plants. *B–E* illustrate the sexual method, effected through an alternation of generations, wherein a vegetative stage, the sporophyte, alternates with a reproductive stage, the gametopyte. (After Shimer.)

as produced by the sterilization of parts originally fertile, *i.e.*, modifications of reproductive tissues. The sporophyte has become increasingly well developed and *increasingly independent*, while the gametophyte has become increasingly simple and *increasingly dependent*. The evolution of plants has proceeded by the progressive development of the sporophyte, and the gradual but steady regression of the gametophyte. This changing relationship is roughly indicated in the following diagram (Fig. 67, and also in Fig. 66).

107. Steps in the Evolution of the Sporophyte.—The

possible steps in the evolution of the sporophyte may, on this theory, be tabulated as follows:[1]

1. Sterilization of fertile tissue.
2. Localization of spore-production in sporangia.
3. Origination of lateral organs (leaves), and of roots.
4. Development of heterospory.
5. Introduction of fertilization by the pollen-tube (*siphonogamy*).
6. Assumption of the seed-habit.

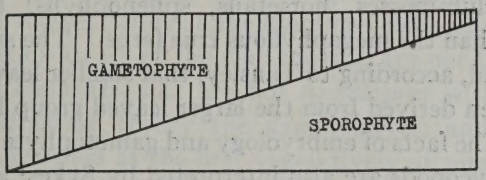


FIG. 67.—Diagram illustrating the gradual change in the relative prominence of the gametophytic and sporophytic phases in the life-cycle of plants during their evolution from the primitive algæ (at the left) to the modern seed-bearing plants (at the right).

108. Second Hypothesis.—In a discussion of Bower's theory, Tansley,[2] considers it "*a priori* in the highest degree unlikely that so fundamentally important an organ as the foliage leaf of the vascular plant appeared in descent as an 'enation' from the surface of a cylindrical body of different morphological nature," and states that "there is no well established case of any such origin of an organ of the importance and with the potentialities of the leaf in the evolutionary history of the plant kindgom." He also calls attention to the fact that the sporophyte (sporogonium) of mosses and liverworts has never been known to produce by enation or otherwise, any structure resembling

[1] Following F. O. Bower.

[2] New Phytologist 7:177–129. April and May, 1908.

a foliage leaf or a sporophyll, and considers that it probably as we now know it, "represents its highest capacity for evolution."

On the hypothesis of progressive sterilization and enation (strobiloid theory), one would expect more primitive sporophytes to possess relatively small leaves, that is, to be *microphyllous*, and those with relatively large leaves (*megaphyllous*) to be of later evolutionary development. But there is no fossil evidence that the microphyllous fern allies (club-mosses, horsetails, sphenophylls) are older groups than the megaphyllous true ferns. The suggestion is at hand, according to Tansley, that smaller leaved forms have been derived from the larger leaved group by reduction. The facts of embryology and gametophyte anatomy of the Lycopods are also interpreted by Sykes[1] as, on the whole, supporting the hypothesis that the simpler Lycopods are reduced forms and not primitive, the entire genus *Lycopodium* being regarded as formed by reduction from some of the larger fossil cone-bearing fern-allies, such, for example, as *Lepidodendron* or one of its near relatives. Miss Sykes has further suggested that the fossil genus *Spencerites* may represent the connecting link, between the two groups.

It is not possible nor essential, in a book of this nature and scope, to give a detailed discussion of the evidence and the literature bearing upon this and similar questions. It is only intended here to call attention to the fact that different inferences as to the origin of the leafy sporophyte and the broad course of plant evolution may be

[1] Sykes, M. G. Notes on the morphology of the sporangium-bearing organs of the Lycopodiaceæ. *New Phytologist.* 7:41–60. Feb. and Mch., 1908.

logically deduced from the same facts, depending on which facts or classes of facts the emphasis is placed.[1]

109. Homologous Alternation.—By the theory of *antithetic alternation* the leafy sporophyte was derived from some such structure as the sporogonium of the Bryophytes, the axis existing first, the leaves originating as outgrowths at its surface. There could thus be no true homology between any of the organs of the sporophyte and those of the gametophyte, however close the superficial resemblance might be. The (gametophytic) leaves of the true mosses, while of like function (*analogous*) to the (sporophytic) leaves of the club-mosses, are not the same structural elements, *i.e.*, are not *homologous* with them. By a contrasting theory the gametophytic and sporophytic stages were at the first vegetatively or somatically equivalent (except for chromosome number), as is the case now, for example, with the red algæ, *Dictyota* and *Polysiphonia*, but, in the course of evolution, the sexual phase became more, and the asexual phase less, important in other forms (*e.g.*, ferns). This is called the hypothesis of *homologous alternation*, since the vegetative organs represent the same structural or morphological elements. According to the antithetic theory the sporophytic phase was originally entirely dependent on the gametophyte (as now, *e.g.*, in the Liverworts), while according to the homologous theory, the sporophyte has been free-living from the start. By the latter theory, also, leaves did not originate as new formations at regions of the axis previously unoccupied by lateral organs (*enation*), but

[1] Those wishing to go more fully into this question will (in addition to the article above cited) find much of the evidence presented and analyzed by Lady Isabel Brown in a series of five articles on "The phylogeny and inter-relationships of the Pteridophyta," in *The New Phytologist* for 1908. An extended bibliography accompanies each article of the series.

axis and foliar organs were both derived from an ancestral thallus, branching dichotomously.[1]

The structural differences in the two generations are, on the basis of this hypothesis, considered as due almost, if not entirely, to differences in environment, the main factor being the gradual transition from aquatic to dry-land surroundings. Where the environment is uniform and the same for both generations, as for *Dictyota*, the gametophyte and sporophyte are identical in external

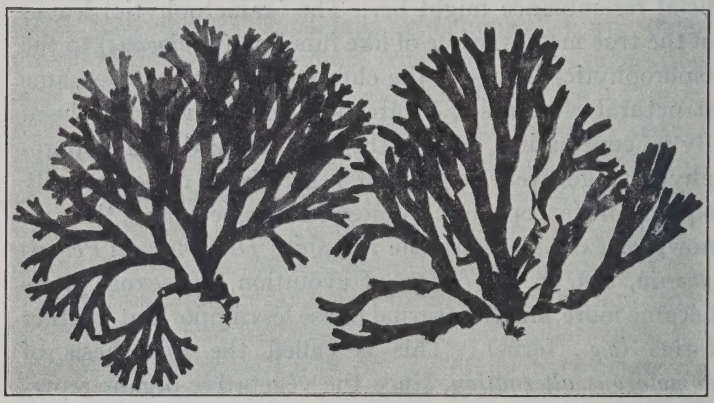


FIG. 68.—*Dictyota dichotoma*. Left, sporogonial plant; right, spermagonial (gametophytic) plant. (After W. D. Hoyt.)

organs and general appearance (Fig. 68). In any event the hypothesis postulates a homology between the various organs of the two generations, however much these parts may differ in external appearance as a result of individual variation and environmental influence.

110. A Third Hypothesis.—Viewing the matter from the standpoint of individual development (ontogeny) Lang has developed the *ontogenetic hypothesis of alternation*.

[1] In a forked manner, resulting from the occurrence of two growing points at the tips of the axes.

From this point of view two alternatives are recognized:

1. Either the fertilized egg and the haploid spore are potentially unlike, and will *therefore* produce unlike plant bodies, even under essentially similar environment, or

2. Fertilized eggs and spores are potentially alike, but produce unlike plant bodies *as a result of the difference in the environment in which they develop.*

The ontogenetic school accepts the latter alternative as a working hypothesis, and regards the gametophytic and sporophytic generations as essentially homologous. The degree of homology which can actually be traced in the vegetative structure of the two generations may vary from substantial identity, as in *Dictyota*, to such wide divergence that the tracing of homologies is quite out of the question. In testing this hypothesis a *crucial experiment* would be to obtain a gametophyte by artificially bringing a fertilized egg to mature development outside of the archegonium and under the environment in which the spores normally develop; or to obtain a sporophyte by causing a spore to develop within the tissue of a gametophyte, as the fertilized egg normally does.

111. Hypothetical Ancestral Tree.—From a comparative study of both living and fossil forms some botanists have been led to infer the common derivation of Filicales, Equisetales, and Lycopodiales from the Hepaticæ, and probably through some form belonging to the Anthocerotales, somewhat as shown in the following ancestral "tree" (Fig. 69). It should be clearly understood that this tree does not illustrate known facts, but only the hypotheses which have been tentatively proposed by careful students on the basis of known facts.

The evidence from fossil forms will be considered more at length in chapters XI and XII.

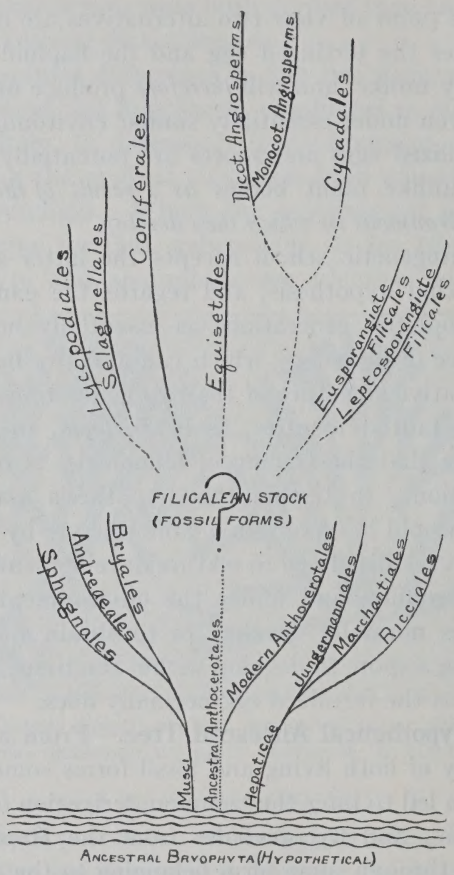


FIG. 69.—Hypothetical genealogical tree to illustrate the probable affinities of the modern plant orders. This diagram is intended to indicate that the plant orders now existing are the tips, only, of the branches of a genealogical tree, whose lower limbs and roots extend into preceding geological periods. Our knowledge is not sufficient to enable us to connect these branches with each other, nor with the main trunk. The diagram teaches that hypothetical (indicated by the dotted line) Anthocerotales gave rise to a now fossil Filicalean stock, from which have been derived all the modern orders above the mosses and liverworts.

CHAPTER X

GEOGRAPHICAL DISTRIBUTION

112. Significance of Geographical Distribution.—From the evidence of comparative anatomy and comparative life histories, and also from the geological record (to be noted later), it has been possible to determine the course of evolution, in broad outlines, with reference to certain of the larger groups of plants. As noted above, we may learn that, in all probability, ferns preceded gymnosperms, and gymnosperms preceded angiosperms; but within these various groups, and for living forms, the problem becomes increasingly difficult. For example, how shall we determine whether the family represented by the bracken fern (*Polypodiaceæ*) is more ancient or more modern than the royal-fern family (*Osmundaceæ*)? Is the maiden-hair tree (*Ginkgo*) a younger or an older species than the pine and the hemlock? Did herbs precede trees in the evolution of Angiosperms, or *vice versa?* This question of the relative ages of living groups is greatly illuminated by the evidence afforded by the facts of geographical distribution of fossil and living forms.

Darwin spoke of geographical distribution as the "almost keystone of the laws of creation,"[1] and one does not need to pursue the study of that subject far to understand the truth of his statement. Before the diffusion of

[1] The interested reader will wish to consult those two remarkable chapters (XII and XIII) of volume two of the *Origin of Species.*

Darwin's teaching, which freed men's minds from the shackles of preconceived notions, founded, not on observation of facts, but on a more or less blind acceptance of current theological suppositions, or on the teachings of ancient writers, the facts of distribution had a far different significance than they were seen to possess when men began to interpret the present state of nature as being the result

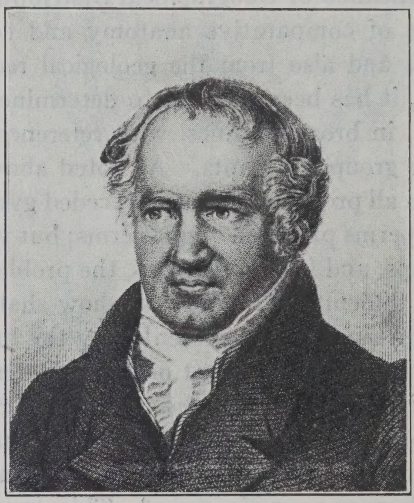


FIG. 70.—Alexander von Humboldt (1769–1859). Founder of the science of plant geography.

of the operation of natural causes; by most students they had been regarded as so much information, like the matter in a guide book, but pointed the way to no larger conception or generalization, so far as historical evolution was concerned. To find giant redwood trees exclusively in California meant nothing, except that they were created there and nowhere else, and had never spread; to find the bracken

fern of almost universal occurrence, in both temperate and torrid latitudes, eastern and western hemispheres, could be easily explained on the supposition that it had gradually spread from the center of distribution where it was created, or on the theory that it had been independently "created" in many different localities.

The idea that the same species was "created" independently in different localities, from which it might spread, was taught by Gmelin as early as 1747. It is often referred to as Schouw's hypothesis, from the Danish botanist who elaborated and urged it in the first part of the nineteenth century.[1] Reasoning from the facts of discontinuous distribution (to be noted in following paragraphs) Schouw argued for the hypothesis of the multiple origin of species, that is, that there were originally many primary individuals. The existing vegetation of the globe was not created at once, argued Schouw, but by degrees, since the surface of the earth has only gradually become fitted for the growth of plants, and moreover certain plants (*e.g.*, parasites) depend upon the existence of others, and therefore the latter must have previously existed.[2] The hypothesis of multiple origin was also, at

[1] Schouw, J. F. *Desedibus plantarum originariis*, Hauniae, 1816. His memoir *On the origin of plants* was published in Danish in 1847, and the English translation by N. Wallich was published in Hooker's *Journal of Botany*, **2**: 321–326, 373–377. London, 1850; and *Ibid*, **3**: 11–14, 1851.

[2] This is an interesting illustration of how the same kind of evidence may lead one student toward the truth and another toward error. Schouw was proposing the ideas here set forth at the same time that Darwin was elaborating his theory of natural selection, and only twelve years before the appearance of the *Origin*. Raising the question as to whether new species continue to be created, or whether the existing vegetable kingdom has been finally completed, he argues that, "The most rational mode for accounting for new species being possibly created, seems to be by suppos-

first, adopted by Alphonse DeCandolle, but finally abandoned by him in his *Géographie Botanique Raisonée* (1855). About the middle of the last century Agassiz was urging his *autochthonous*[1] hypothesis, namely, that each species originated where it is now found (indigenous), covering from the first as large an area as at present. This hypothesis, if true, would, as Gray pointed out, "remove the whole question out of the field of inductive science." There would be no incentive to study the question of geographical distribution, and little of value could result from such an investigation. Both Schouw's and Agassiz's ideas have long since been abandoned. It is no longer considered a matter of hypothesis or theory, but of well established fact, that most of the existing species are immeasurably older than the present configuration of the continents; in fact many genera and families of Angiosperms of the present land flora were clearly defined as early as the Tertiary period, and have undergone little change since that remote time.

113. Means of Dispersal.—The question of the means of dispersal of the seeds and spores of plants is a large one, and a voluminous literature exists on the subject. This is not the place to go extensively into the matter, but a dis-

ing that a change of climate or soil produces a corresponding change in the character of its plants; or that some casual difference in the character of the type of any given plant, may have become permanent by its being isolated. It is in this way that constant varieties have arisen, which may sometimes even have become real species, but on all these occasions it is culture that has been the cause; as far as I know, we possess no facts to prove that natural causes have produced this effect." Schouw also reached the erroneous conclusion that the present flora was probably *not* derived from the plants of preceding geological periods.

[1] Autochthon, from the Greek *αὐτός, self* + *χθών land*, meaning *from the land itself.*

cussion of geographical distribution requires a clear understanding of certain points which may be briefly alluded to here. The situation with plants is, of course, quite different than that with animals. With the advance of a continental ice sheet, for example, animals may actively retreat, by their own locomotion. There are exceptions to this method of animal dispersal. Insects and small birds may be blown by the wind over considerable distances, and insect eggs, larvæ, and cocoons may be transported in the soil about the roots of floating uprooted trees and otherwise; and instances are on record of animals being carried as passengers on floating objects, notably, according to Semon, in the Malay Archipelago; snakes and crocodiles are known to have drifted in this way to the shores of the Cocos or Keeling Islands, a group of coral atolls in the Indian Ocean, about 700 miles southwest of Java, the nearest land.

But plants, at all times and under all circumstances, are wholly dependent on being carried passively by external agencies. The chief means of seed dispersal are the *wind, streams and ocean currents,* and *animals*—particularly birds. For distribution over great distances it is of importance to consider chiefly wind, ocean currents, and birds.[1]

114. Dispersal by Wind.—DeCandolle, the great Swiss student of plant geography, regarded the wind as "the most general and ordinary cause of the distribution of species over the entire surface of a country," but rejected it as a means of dispersal over even narrow arms of

[1] The distribution of seeds in connection with commercial shipments is interesting, but not essential to our present purpose. The word "seeds" is used above to designate all reproductive bodies, including fruits, spores, and vegetative reproductive bodies, such as gemmæ, bulbils, etc.

the sea. "I have never heard," he said,[1] "of a single seed carried from England to France, nor from Ireland to England by the agency of the west winds, although they are so intense and so frequent in those countries. I do not believe it has ever been demonstrated that seeds have

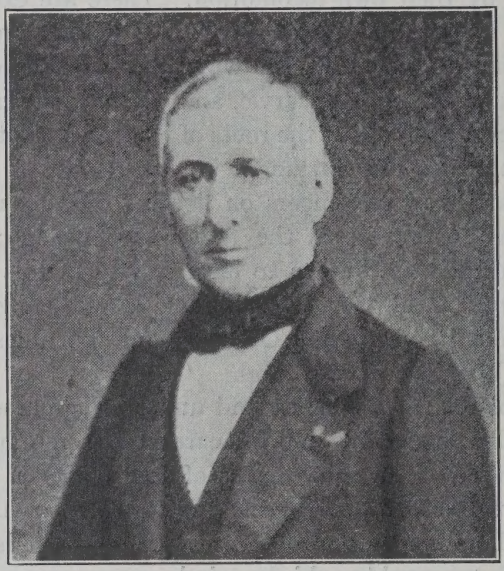


FIG. 71.—Alphonse De Candolle (1806–1893). Noted Swiss botanist and student of plant geography. Author of *Géographie Botanique Raisonée.* (From *Acta Horti Bergiani.*)

fallen in Sardinia from Africa, in Corsica from Sardinia, nor from Corsica to the coast of Genoa and Nice, although the south winds are there very violent." Other students have reached the same conclusion on similar *negative* evidence. It has also been argued, on general grounds,

[1] *Géographie Botanique Raisonée* 2:614. Geneva, 1855.

that the rate of fall of various seeds in air is such that they would have to be carried to improbable heights by the wind in order to travel for very great distances before falling to the ground.

But no amount of negative evidence is conclusive in the face of even one firmly established bit of positive evidence, and the positive evidence is not only more conclusive but more voluminous than the negative. Seeds of the pitcher plant, *Nepenthes ampullaria*, are known to have been transported from Ceylon to the Seychelles, a distance of 1500 miles, and Engler calculated that, out of a total of about 675 species in Hawaii, 140 ferns and other spore-bearing plants, and 14 angiosperms were quite certainly transported thither by wind. In fact, a large percentage of the vegetation of isolated oceanic islands is of plants whose seeds could hardly have been transported there in a viable condition except by winds.[1]

As Warming has noted, there is not an oceanic island destitute of plant life, though many of them are separated from the present mainland by hundreds and even thousands of miles of salt water, and have never, in all probability, been connected with any continent; all their vegetation, therefore, must have been transported thither by some agency. In 1901 there fell in Switzerland large quantities of dust which is said to have undoubtedly come from Africa. If this were possible it is certainly not improbable that light seeds of various species might be transported very long distances in a similar manner. The

[1] Even small animals, and especially insects, are known to be transported to considerable distances by the wind. During his voyage on the exploring ship *Beagle* (1832–1836), Darwin observed spiders, buoyed up by their webs, being wafted over the vessel by the wind as far as 60 miles from land.

wind is known to be a factor in plant-distribution in the West Indies. Thus, for example, previous to 1899, the sedge, *Fimbristylis spathacea* Roth, was not known on Great Bahama island, of the West Indies. After the hurricane of August 13, 1899 this sedge appeared in clearings, and "soon spread as a troublesome weed through cultivated lands, killing out pasture grass in places; it had therefore come to be called 'Hurricane Grass."[1]

In August, 1883, the island of Krakatoa, west of Java in the Sunda Strait, experienced a terrific volcanic eruption, which completely destroyed every vestage of its vegetation, converting the green island into a desolate desert. Within three years thereafter Treub found growing there six algæ and 26 vascular plants, including 11 ferns and 15 spermatophytes. A little over ten years after Treub's visit Penzig found 62 vascular plants, of which 60 per cent. had been brought by ocean currents, 32 per cent. by wind, and 7 per cent. by fruit-eating birds. Within twenty-five years from this eruption the island was again green with forest growth and other vegetation, and in 1906 a party of botanists confined their collecting to a narrow zone of forest near the shore *because of the difficulty of "cutting a way through the dense growth of tall grasses"* between the shore and the volcanic cone in the center of the island. Among the means of transportation of plant life to Krakatoa, the wind is regarded by Ernst as a factor of exceptional importance. Up to 1906, as calculated by him, 39–72 per cent. of the total number of phanerogams on the Krakatoa group were brought by ocean currents. Ten to 19 per cent. of the entire flora by birds, and 16–30 per cent. by air-currents. Beccari found the same

[1] Britton & Millspaugh. Bahama Flora., p. 51. Unpublished.

species on widely separated mountain tops in the Malay Archipelago where wind (particularly the west monsoon) is the only agent of dispersal that may reasonably be assigned. The seeds of many plants are as light as dust particles, and it has been calculated that nearly 850,000,000 tons of dust are transported as far as 1,440 miles a year in the western United States.[1] In the light of this information it is not difficult to understand how seeds of *Nepenthes phyllamorpha*, that weight only 0.000035 gram, seeds of *Rhododendron verticillatum* and of *Dendrobium attenuatum*, that weigh 0.000028 gram and 0.00000565 gram respectively, can be transported many miles, resulting in a geographical distribution of those (and various other) species, on the mountain tops of oceanic islands that are miles apart.

James Small has carried out a series of painstaking experiments on the transportation of the seeds of various plants by artificially produced air currents. Among many valuable results of these experiments, he determined that for the seeds of the dandelion, "so long as the relative humidity of the air remains above 0.77 per cent. and so long as the fruit does not encounter an obstacle, a horizontal wind of 1.97 miles per hour is sufficient for its dispersal to any distance. If the air becomes moist the pappus closes up and the fruit falls rapidly." Small further concludes that the ordinary pappose fruit of the Compositæ, under the proper meteorological conditions, can be blown many hundreds of miles over land and sea, and "that hypothetical land bridges are not necessary to explain the present distribution of the Compositæ, so that we can take the world

[1] Cited by James Small (*New Phytologist* **17**: 226. 1918) from Evans, J. W. The wearing down of rocks, Pt. II, *Proc. Geol. Assoc.* **25**, Pt. 4: 229. 1914.

as it is without raising and sinking continents, as Darwin says, 'in a quite reckless manner.' This latter is an important point, as the Compositæ are almost certainly of such recent origin that the possibility of land bridges is in many cases quite out of the question." In fact, Small contends that a "rational study of the history of the Compositæ, their migrations and colonizations, their paths of travel and regions of concentration," is not possible without a correct understanding of the conditions of wind dispersal.

The occurrence of a species of *Senecio* (a pappose-fruited Composite) on the Falkland Islands, 300 miles from the nearest land, and of another species on St. Helena and on Prince's Island, nearly 1500 miles from the nearest land, are attributed by Small respectively to the westerly and the south-east trade winds. The distribution of the family, as worked out in detail by Small[1] affords an instructive illustration of how geographical distribution affords new evidence and confirms other evidence as to the relative ages of various related groups of plants, and as to the fact and course of evolution within a given plant family. The immense genus, *Senecio*, for example, according to Small, comprising over 2300 species, is of very wide distribution, being marked by a concentration at high altitudes, which is not surprising in a wind-distributed group.[2] Some of the species are widespread, and some are local, and the group is characterized by its ready response to the influence of environment; to this is attributed, in large part, its great morphological variation. No species covers the range of the genus.

[1] Small, James. The origin and development of the Compositæ. Chapter X. *New Phytologist* **18** : 1–35. Jan. and Feb., 1919.

[2] It has been calculated by Ball that 25–30 per cent. of the flora of the higher Andes are Composites.

Small has shown that the local species have regions of concentration along the paths of migration of the widespread species, and that they are most abundant "along the ridge which extends around the Pacific and Indian Oceans from Tierra del Fuego to South Africa." The paths of migration are chiefly coextensive with the altitude of 3,000 ft., or higher, and all the facts point to the Andes of Bolivia as the probable (hypothetical) center of distribution for the genus, whence it has rapidly spread "along the unwooded regions of the mountain ranges of the world." This world-wide distribution, and the possession of pappose fruits which would make possible a wide distribution in a relatively short period of time (geologically speaking), all point (as do the facts of its morphology) to the comparative youth of the group; while its marked tendency to variation, its success in the struggle for existence (as may be noted everywhere), and finally the existence of innumerable *local* species, with centers of distribution *along the paths of migration of the genus as a whole,* are just the facts which one would expect to find on the basis of the theory of evolution.

115. Dispersal by Water and Birds.—Space at our disposal will permit of only a passing reference to seed-dispersal by water and birds. In order to be carried for long distances by water, seeds and spores must be able to undergo prolonged soaking in water, and in the case of ocean currents, in salt water. Many species of the new strand flora of Krakatoa were certainly brought many miles by ocean currents, and Guppy, who made a study of "Plants, seeds, and currents in West Indies and Azores,"[1] cites the case of a ragweed (*Ambrosia crithmifolia*) whose

[1] Guppy, H. B. London, 1917.

seeds were dispersed on floating logs; and the small seeds of several species were safely transported in the crevices and holes made in small stems and branches by worms and molluscs. Other seeds were floated on blocks of pumice.

In Hawaii, while nearly 85 per cent. of the spermatophyte flora is endemic (see p. 165), about 70 per cent. of the species of the coastal zone are introduced. This is in marked contrast to the general rule for oceanic islands, whose littoral floras, as might be expected, are predominantly cosmopolitan. In this particular case MacCaughey attributes very great importance to ocean currents as agents of dispersal. The natives of these islands, at the time of their discovery, are reported to have had large canoes hewn from tree trunks of the Douglas spruce, which could have come only from the northwest shores of North America; and considerable numbers of tree trunks and large branches are brought from the same coasts to Hawaii each year. Ocean currents also bring annually large quantities of plant material to the coast of other oceanic islands. Tansly and Fritsch have noted large numbers of young seedlings and germinating seeds in drift material on the coast of Ceylon, and Moseley observed many living plants in the coastal drift of the Moluccas, including trees, palms, epiphytic orchids, and large quantities of fruits containing viable seeds.

Seeds are carried by birds in mud adhering to their feet, lodged in their feathers, and in the alimentary canal. In mud adhering to the feet of a partridge Darwin found 82 seeds that germinated. Wallace is authority for the statement that "all the trees and shrubs in the Azores bear berries or small fruits which are eaten by birds; while all those which bear larger fruits, or are eaten

chiefly by mammals—such as oaks, beeches, hazels, crabs, etc.—are entirely wanting.[1] It has been suggested by both Guppy and Schimper that the wide distribution of fig trees in oceanic islands (*e.g.* Malay and Solomon Archipelagos) is due to their fruit being eaten by doves and other birds capable of sustained flight. The prodigious powers of flight of some of the migratory birds would make them, theoretically at least, most efficient agents of seed dessemination over wide areas. The scarlet tanager, for example, breeds in the eastern United States from Oklahoma to the mountains of North Carolina, and north to New Brunswick and Saskatchewan. At the close of summer the birds migrate south, passing from the Gulf coast of the United States to and along Central America to the west tropical coast of South America. The arctic tern nests during the northern summer along the northeast arctic coast of North America and the southwest coast of Greenland, but passes the northern winter within the Antarctic Circle, 11,000 miles away. Passing as it does through regions of similar climate in the northern and southern hemispheres, it would theoretically be possible for spores and light seeds to be carried to congenial habitats on both sides of the equator. The American golden plover breeds in summer along the northern coast of Canada, the parallel of 70° north latitude passing approximately through the center of its breeding range. In early fall the birds migrate to Labrador, thence to Nova Scotia, and thence, after a few weeks, in a straight flight of 2,400 miles to the north coast of South America. From their landing point the birds pass to Argentina where they pass the northern winter,

[1] Wallace, A. R., *Darwinism*, 3d edition, p. 361.

returning the following spring to the Arctic coast, but by an entirely different rout, passing over Central America, the Gulf of Mexico, and across central North America.

The Pacific golden plover nests along the arctic shore of Eastern Siberia and the western coast of Alaska, but winters in southeastern Asia, eastern Australia and generally in the islands of Oceanica, the winter home having an east-west range of about 10,000 miles. The journey from Alaska to Hawaii, a distance of some 3,000 miles, is made in a single flight.[1] Whether seed dispersal is actually accomplished by any of the above long distance travelers is not definitely known to the writer; but the flights are accomplished in a comparatively brief period, and it seems not unreasonable, from what we actually know of seed-transportation by birds, that lighter and more resistant seeds and spores of plants may be thus, transported, concealed in the plumage of the birds, or otherwise, and between stations where no other known agent of dispersal would appear to be adequate.

In 1911 a violent eruption of the Taal Volcano, on Volcano Island, Luzon, Philippine Islands, "annihilated" (as Maso described it) every vestage of vegetation on the island. The destruction was caused by superheated steam, and by the deposit of a layer of fine "mud," which fell like rain, and carried with it large quantities of sulphur dioxide and possibly other substances fatal to plant life. In a study of the revegetation of the island, made six years after the eruption, Brown, Merrill, and Yates found evidence that birds were the most important

[1] For the above data on bird migrations the author is indebted to the article on "Our greatest travelers," by Wells W. Cooke. *Nat. Geographic Mag.* **22** : 346–365. April, 1911.

agents of transportation of seeds for the new growth, about 54 per cent. of a total of 157 species having seeds adapted to dispersal by birds, only 21 per cent. adapted to wind dispersal, and only 9 per cent. apparently brought by currents of water. Of course, the distance from Volcano Island to the nearest uninjured vegetation was short, and the various agents of dispersal would, no doubt, assume a different relative importance for greater distances, as they did, for example, in the case of Krakatoa, noted above.[1]

116. Struggle for Existence a Factor.—DeCandolle early contended that it was not sufficient that one or even a few seeds be carried to a country already well covered with vegetation in order for the new arrivals to become established, but that a very large number of vigorous seeds must be introduced to insure success in the struggle for existence with the native plants. Attention has been called in a preceding chapter (pp. 94–96), however, to the enormous rate of propagation of plants and animals, which proceeds in geometrical progression; so that if we allow a sufficient time period, and postulate a species suited to the climate and soil of its newly found home, we may expect a large degree of success in its be-

[1] In contradiction to the above statements of fact and logical inference, there should be noted here Warming's quotation (*Botany of the Faeroes*), p. 676. London, 1901–1908) from the Danish Zoologist, H. Winge, of the Zoological Museum, Copenhagen, who stated in a letter to Warming that he had carefully examined thousands of migratory birds picked up dead at Danish lighthouses, and had never found any seeds adhering to the feathers beaks, or feet. Dried mud was found "fairly often," but there were adhering to it no seeds large enough to be seen with the naked eye or the hand-lens. Moreover the stomachs of migrating birds were always found to be practically empty, indicating that migrating birds travel on empty stomachs. See, however, p. 164, *infra*.

coming established, at least in limited area and numbers, even though the number of seeds introduced was comparatively small. Farmers in America can bear emphatic but sad testimony to their practical helplessness to combat successfully the spread through the hay fields of the hated daisy or white-weed (*Chrysanthemum leucanthemum*), or the still more dreaded Devil's paint brush (*Hieracium aurantiacum*). Both of these species are now common weeds in America, though introduced from Europe, the former almost, and the latter quite within the memory of men now living. Wallace has stated that, if a million seeds were brought to the British Isles by wind in one year, there would be only ten seeds to a square mile. "The observation of a life time might never detect one, yet a hundredth part of this number would serve in a few centuries to stock an island like Britain with a great variety of continental plants." When we recall the enormous mortality of seeds and seedlings, such facts as these enable us to appreciate the importance to a species of an abundance of spore and seed production, as, for example, in dandelions and other composites, in ferns, and indeed in most plants.

117. Types of Distribution.—There are two broad types of geographical distribution; *continuous*, as in the case of the bracken fern (*Pteris acquilina*); and *discontinuous*, as in the case of the *Osmunda* family, where a given species is found in widely separated localities, but not in the intervening regions. *Osmunda regalis* (the Royal Fern), for example, is known from eastern North America, central and northern Asia, and Europe; *Osmunda Japonica* from central and northern Asia and Japan and the cinnamon fern (*Osmunda cinnamomea*) only from eastern North America and Japan. The genus *Diervilla*,

of the Honeysuckle family, is represented in the eastern United States and Canada by the bush-honeysuckle (*Diervilla Lonicera*), and in the mountains of the southern States by *D. sessilifolia* and *D. rivularis*; it is not found elsewhere except in eastern Asia, where it is represented by the shrubs commonly cultivated in temperate America under the name *Weigela*.

In the herbarium of the Brooklyn Botanic Garden are two specimens of the cloud-berry, or mountain bramble (*Rubus chamæmorus*), collected in a bog near Montauk

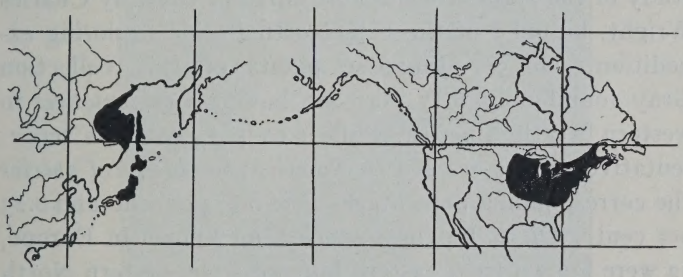


FIG. 72.—Map showing the geographical distribution of the skunk-cabbage, *Symplocarpus fœtidus*. (After M. L. Fernald.)

Point, Long Island, by Dr. William C. Braislin, in 1908. This is an arctic and sub-arctic bog plant, ranging from Labrador and Newfoundland to New Hampshire, British Columbia, and Alaska; also in Europe and Asia. It was found on the Peary arctic expedition as far north as Lat. 64° 15′ north. Its discovery as noted above was unexpected, and affords an interesting example of discontinuity of distribution. Another striking illustration is the "curly grass" fern (*Schizæa pusilla*), of the Polypodiaceæ, found in Nova Scotia and Newfoundland, and in the pine barrens of southern New Jersey, but not known to occur between

these two regions. The skunk-cabbage (*Symplocarpus fœtidus*, Fig. 72), species of *Magnolia*, *Hydrangea*, *Hamamelis* (witch-hazel), *Liquidambar* (sweet-gum), *Aralia* (ginseng), *Eupatorium*, *Onoclea* (sensitive fern), *Lycopodium* (*L. lucidulum*), and scores if not hundreds of other species, have a similar type of distribution.

Similarity of Floras of Eastern Asia and Eastern North America.—The similarity in the floras of eastern North America and eastern Asia and Japan was first pointed out by Asa Gray,[1] in 1859, on the basis of his study of the plants collected in Japan in 1855, by Charles Wright, botanist of the U.S. North Pacific exploring expedition. Of 580 Japanese plants of this collection Gray found only 0.37 per cent. having *representatives* in western North America, while 0.61 per cent. has representatives in eastern North America; for *identical species* the corresponding percentages were 0.27 per cent. and 0.23 per cent. Of 56 Japanese species not known in Europe, 22 were known from eastern but not from western North America. Exploration subsequent to the date of Gray's paper has altered our knowledge of the distribution of many species in the region referred to, but the broad fact pointed out by Gray has only been confirmed by more careful investigation.

Several writers[2] have called attention to the fact that various species of plants and of invertebrate animals are confined to the west of Ireland and North America.

[1] Gray, Asa. On the botany of Japan, and its relations to that of North America, etc. Botanical Memoirs, extracted from Vol. VI (New Series) of the *Mem. Amer. Acad. Arts* and *Sciences*. Boston and Cambridge, 25th April, 1859.

[2] *E.g.*, Colgan, N., and R. W. Scully. *Cybele Hibernica*. 2d Ed. p. 71. Scharff, R. F. *Proc. Royal Irish Acad.* **28**: 13. Nov., 1909.

Among the plants may be mentioned ladies' tresses (*Spiranthes Romanzoffiana*) and the seven-angled pipewort (*Eriocaulon septangulare*); and among animals, the land snail, *Helix hortensis*.

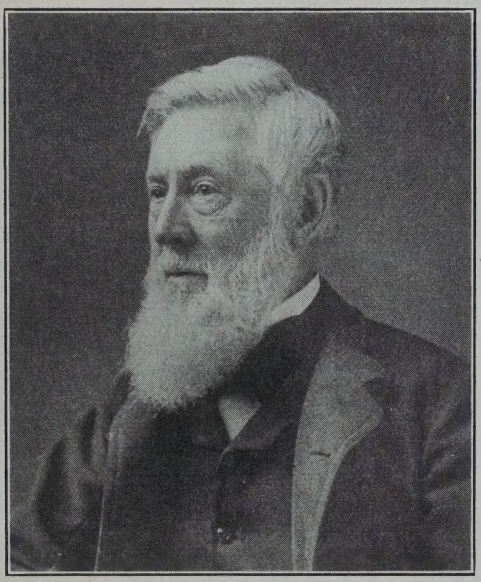


FIG. 73.—Asa Gray (1810–1888). Noted American botanist and student of plant geography.

Of the various theories which have been advanced to explain the occurrence of identical species on opposite shores of the North Atlantic, Scharff enumerates the following three.[1]

1. Migration from Europe across Asia and a Bering Strait land-bridge to America, or *vice versa*.

[1] Scharff, Robert Francis. On the evidences of a former land bridge between northern Europe and North America. *Proc. Royal Irish Acad.* **28B**: 1–28. Nov., 1909.

2. Occasional transport by birds across the Atlantic Ocean.

3. Migration across a direct Atlantic land-connection. Human agency is generally rejected, except in cases where it can positively be demonstrated.

In interpreting the above facts Scharff argues that "the interchange between the fauna and flora of north-western Europe and north-eastern America was effected across the northern land bridges," which the facts of distribution and other evidence indicate existed in pre-Glacial times, and probably in late Pliocene and early Pleistocene.

Numerous alpine species have a present discontinuous distribution in the lowlands of arctic and sub-arctic latitudes, and on lofty mountain peaks, widely separated, in more southern latitudes. Darwin called attention to the fact that "a list of the genera of plants collected on the loftier peaks of Java raised a picture of a collection made on a hillock of Europe;" and again that "certain plants growing on the more lofty mountains of the tropics in all parts of the world, and on the temperate plains of the north and south, are the same species or varieties of the same species." A striking illustration of this latter fact is the small white water-lily (*Castalia tetragona*), which is found along the Misinaibi and Severn rivers in Ontario (Canada), and at Granite Station, in northern Idaho (U. S. A.), but is not known elsewhere except in Siberia China, Japan, and the Himalaya mountains (Kashmir).

The flora near the summit of Mt. Washington and other peaks of the White Mountains, in New Hampshire, has elements in common with that of Labrador. "In approaching these mountain summits," says Flint,[1] "one

[1] Flint, William F. The distribution of plants in New Hampshire. In Hitchcock, C. H. *The Geology of New Hampshire*, 1: 393. 1874.

is struck by the appearance of the firs and spruces, which gradually become more and more dwarfish, at length rising but a few feet from the ground, the branches spreading out horizontally many feet and becoming thickly interwoven. These present a comparatively dense upper

FIG. 74.—Lapland rhododendron (*Rhododendron lapponicum*). Photographed on the summit of Mt. Madison, New Hampshire, June 25, 1917, by Ralph E. Cleland.

surface, which is often firm enough to walk upon. At length these disappear wholly, and give place to the Lapland rhododendron (Fig. 74), Labrador tea, dwarf birch, and alpine willows, all of which, after rising a few inches above the ground, spread out over the surface of the

nearest rock thereby gaining warmth, which enables them to exist in spite of tempest and cold. These in their turn give place to the Greenland sandwort, the diapensia (Fig. 75), the cassiope, and others, with arctic rushes, sedges, and lichens, which flourish on the very summit."[1]

According to Flint, there are about fifty strictly alpine species on these summits, found nowhere else in New England and New York, except on similar summits, such as Mt. Katahdin in Maine, and Mt. Marcy and Mt. McIntyre in New York State.

Incidentally, it may be remarked that a similar statement may be made for the animal life. Writing of the insects, Scudder says[2] that, "in ascending Mt. Washington, we pass, as it were, from New Hampshire to northern Labrador; on leaving the forests we first come upon animals recalling those of the northern shores of the Gulf of St. Lawrence and the coast of Labrador opposite Newfoundland; and when we have attained the summit, we find insects which represent the fauna of Atlantic Labrador and the southern extremity of Greenland."

118. Effects of Continental Glaciation.—The above mentioned and other similar cases of discontinuity are satisfactorily explained by the advance and retreat of the

[1] Among numerous species that have been recorded from both Labrador and the peaks of the White Mountains, there may be mentioned the following: *Salix argyrocarpa, S. phylicifolia, S. herbacea, S. uva-ursi, Comandra livida, Arenaria groenlandica, Silene acaulis, Oxyria digyna, Cardamine bellidifolia laxa, Saxifraga rivularis, Sibbaldia procumbens, Empetrum nigrum, Epilobium Hornemannii, Loiseleuria procumbens, Rhododendron Lapponicum, Phyllodoce coerulea, Cassiope hypnoides, Arctostapphylos alpina, Vaccinium cæspitosum, Diapensia Lapponica, Veronica alpina* var. *unalaschensis, Gnaphalium supinum.*

[2] Scudder, Samuel H. Distribution of insects in New Hampshire. In Hitchcock, C. H. *The geology of New Hampshire,* 1 : 341. 1874.

continental glacier during the Ice Age. With the advance of the ice all vegetation was either exterminated or compelled to migrate southward. With the subsequent retreat of the ice northward the glaciated region was gradually re-occupied by the encroachment of vegetation from the south, and of this flora the arctic species could become permanently re-established only in what are now the arctic regions, and in the arctic or sub-arctic climate of the higher mountain tops, forming there what is known as a *relict* flora.[1] It has been suggested that, in theory, alpine plants on high mountain peaks south of the region covered by the continental ice sheet, should not be related to arctic and sub-arctic forms. In harmony with this idea Wallace has cited the volcanic Peak of Teneriffe (Pico de Teyde), in the Canary Islands, 12,000 feet high, where, above the timber line, von Buch found only eleven species of plants, eight of which appeared to be endemics; but all of them were related to the plants of the same general region, growing at lower levels.

However, seed-distribution by birds and winds and other agencies has been going on continually since the continental ice sheet began to recede, with the result that arctic-alpine and subarctic-alpine plants are numerous in the alpine zone of higher peaks below the southern limits of continental glaciation. Thus the snowy cinquefoil (*Potentilla nivea*) is found, not only throughout the arctic regions, but also in the Alps, in alpine Asia, and in the Rocky Mountains as far south as Utah and Colo-

[1] The effect of continental glaciation on the distribution of plants was first noted by Edward Forbes, but was also worked out independently by Darwin several years previous to the publication of Forbes's paper. (Darwin, C. *Life and Letters*, 1 : 71–72, 372. New York, 1901. See also *The Origin of Species*, 2: 152. New York, 1902.)

rado. According to Rydberg[1] there is evidence that it has spread not only in the earlier postglacial period, but also in recent years. The common arctic and sub-arctic grass, *Phleum alpinum*, occurs as far south as Arizona and

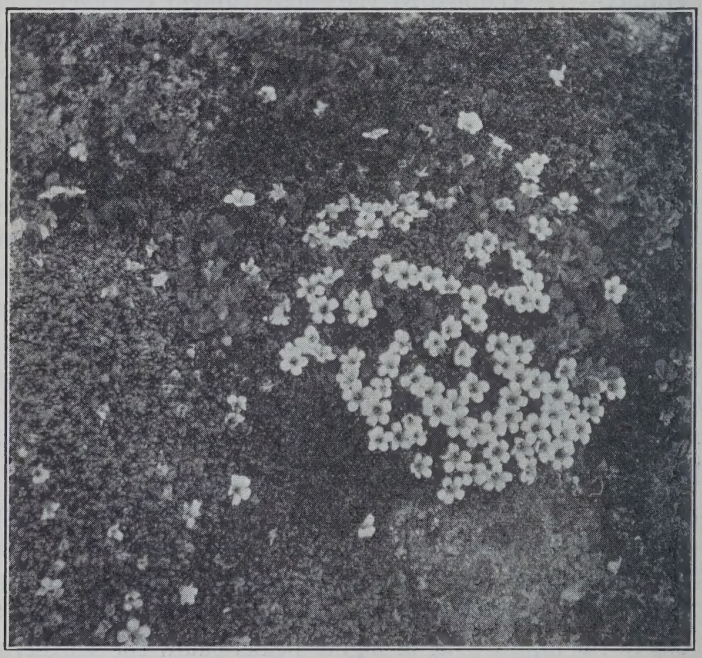


FIG. 75.—*Diapensia lapponica*. Photographed on the summit of Mt. Madison, New Hampshire, June 25, 1917, by Ralph E. Cleland.

California and the Sierra Madre of Mexico, and also in Patagonia. It is also found throughout the Montane zone, from which it might have spread to the subalpine, following the woods throughout the whole mountain system. Other similar cases might be cited.

[1] Letter from Dr. P. A. Rydberg to the author.

119. Escapes from Cultivation.—Every case of discontinuous distribution must be carefully analyzed by itself, and care must be taken not to adopt unwarranted conclusions. Thus, certain cases of discontinuity are explained by the escape from cultivation of forms introduced by human agency for economic uses, and thus have no scientific significance. The presence in the Hawaiian Islands of such economic plants as sugar-cane, cocoanut, and others is an apparent case of discontinuity, but these plants are known to have been introduced there by man, and to have escaped from cultivation. Campbell thinks that the candle-nut tree (*Aleurites moluccana*, the source of a commercial oil) and the mountain apple (*Eugenia malaccensis*), which now constitute the chief elements in the lowland forests of Hawaii, were also introduced by man, and are therefore only apparent cases of discontinuity. Among numerous illustrations of this in North America may be mentioned the paper mulberry (*Brousonetia papyrifera*), white mulberry (*Morus alba*), hemp, (*Cannabis sativa*), stinging nettle (*Urtica dioica*), the day lily (*Hemerocallis fulva*), all natives of Europe and Asia, and the tree, *Paulownia*, a Japanese species now becoming established as an escape from cultivation in New York, New Jersey, the District of Columbia, and Georgia. The last two species were introduced into North America as ornamental plants, the hemp and white mulberry, of course, as economic plants, the latter in connection with the raising of silk worms.

Attention has recently been called to the wide and rapid spread of the Japanese honeysuckle (*Lonicera japonica*) introduced in the Eastern United States from Asia. Twenty-five or thirty years ago this was a comparatively

rare cultivated vine, but since that time, according to Miss Andrews,[1] "it has spread over practically the whole of the Eastern States, from the Gulf of Mexico to the estuary of the Hudson, making itself equally at home in the low hammocks of the Coastal Plain, on the old red hills of the Piedmont region, on the stony ramparts of the Lookout Plateau, and onward for a thousand miles up the great Appalachian Valley." The adaptability of the plant, as indicated by this description of its habitats, in no doubt a large factor in its rapid spread, for while it is a profuse bloomer under cultivation, it tends to become weedy, as it grows wild, blossoming rarely and therefore setting few seeds. But its wide distribution must have been accomplished by the dissemination of its seeds, and in this Miss Andrews believes that the most probable agents are birds, to whose feet the small, inconspicuous nutlets, "embedded in a mucilaginous pulp," readily adhere.

Several species (*e.g.*, the fleabane, *Pluchea fœtida*) are found in shallow fresh water or fresh or salt water marshes from southern New Jersey to Florida, and then across 120 miles of salt water in Cuba. In this case it seems clearly evident that the seeds have been able to undergo transportation across the Florida strait within comparatively recent times. Examples might be multiplied, and in such cases discontinuous distribution has little evolutionary significance for the particular species concerned, though the facts may serve to throw light upon other cases that are significant.

120. Endemism.—On the basis of the evolution theory every species originated in some one area (its center of dis-

[1] Andrews, E. F. The Japanese honeysuckle in the Eastern United States. *Torreya*, **19**: 37–43. Mch. 1919.

tribution), where it was at first endemic,[1] and whence it gradually spread as far as it could. This is well illustrated in the distribution of the Verbenaceæ, one of the higher and therefore more recent families of flowering plants, comprising about 75 genera and 1300 species, occurring widely throughout tropical and temperate regions. Of 104 species belonging to various genera in the Philippines, 60 per cent., according to Lam,[2] are apparently endemic. These endemic forms have undoubtedly been derived from the 39 non-endemic species, and will, in the course of time, spread from the Philippines to neighboring islands and thence to the mainland. About 85 per cent. of the flora of Hawaii is endemic,[3] and even the strand flora, while cosmopolitan on the whole (the general rule for coastal vegetation), is nearly 40 per cent. endemic, a surprisingly high percentage.

From the facts of geographical and geological distribution, Wallace deduced the following law:[4] *Every species has come into existence coincident both in time and space with a pre-existing closely allied species.*" "The law here enunciated," said Wallace, "not merely explains but necessitates the facts we see to exist, while the vast and long-continued geological changes of the earth readily account for the exceptions and apparent discrepancies that here and there occur." And again, "this law agrees

[1] *Endemic*: found in a given region, but not elsewhere.

[2] Lam, H. J. The verbenaceæ of the Malayan Archipelago. Groningen, 1919.

[3] Including, for example, all the native Hawaiian palms, belonging to the genus *Pritchardia*. See MacCaughey, Vaughan. *Bull. Torrey Bot. Club*, **45**: 259–277. July, 1918, and *Plant World* **21**: 317–328. Dec., 1918.

[4] Wallace, Alfred Russel. On the law which has regulated the introduction of new species. *Annals and Mag. of Nat. Hist.* **16**, Ser. 2: 184–196. Sept. 1855.

with, explains and illustrates all the facts connected with the following branches of the subject: 1st, the system of natural affinities; 2d, the distribution of animals and plants in space; 3d, the same in time . . . 4th, the phenomena of rudimentary organs." And Wallace goes on to show, in detail the bearing of the law upon each of the four points enumerated.

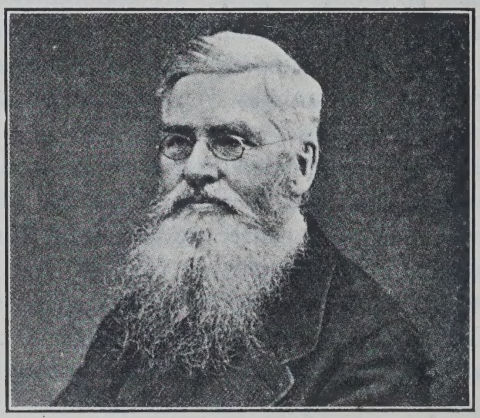


FIG. 76.—Alfred Russel Wallace (1823–1913). Co-discoverer, with Darwin, of the principle of natural selection. Noted student of geophical distribution.

A quotation from Darwin is also pertinent here: "It is . . . obvious," said Darwin, "that the individuals of the same species, though now inhabiting distant and isolated regions, must have proceeded from one spot, where their parents were first produced for, as has been explained, it is incredible that individuals identically the same should have been produced from parents specifically distinct."

121. Mutation and Discontinuous Distribution.—Reading Darwin's statement in the light of the mutation theory

of de Vries, we must of course recognize that, if a mutating species were widely distributed, different individuals of the species in widely separated localities and even with a discontinuous distribution, might throw the same mutants. *Œnothera Lamarckiana*, for example, threw the same elementary species (mutants) in experimental pedigree cultures in Holland and in various localities in the United States.[1] Had *O. Lamarckiana* (contrary to fact) been widely distributed in nature, such mutants as *O. gigas*, *O. scintillans*, *O. lævifolia*, and others would possibly (or even probably) have appeared in different and widely separated stations, and these elementary species might conceivably (and not improbably) have become established as true species of the systematist. When, therefore, we find a given species (or a larger group) in widely separated localities, but not in the intervening regions, we must (barring the phenomenon of mutation referred to above) conclude, either that it has been able to migrate across barriers where it could not become established (as when seeds of land plants are carried by ocean currents across barriers of salt water), or else it has formerly had a continuous distribution, but has subsequently died out in regions between its present localities; in the latter case it is referred to as a *relict endemic*. When these localities are distant hundreds or, as is often the case, thousands of miles from each other, one can readily understand that species having such discontinuity of distribution must, other things being equal, be older than species having continuity of distribution; they must have existed long enough for the changes above mentioned to have taken place.

This principle is confirmed by the evidence of fossils. A striking case is that (cited by Chodat) of *Zelkowa*,

[1] See pp. 114–117.

related to our modern elms. This genus comprises only four living species, which occur in only three widely separated areas, namely, the far East (Eastern China and Japan), the area between the Black and the Caspian Seas (Caucasia), and islands in the eastern Mediterranean Sea. But a study of the fossil evidence shows that during a preceding geological age this genus had a very extended distribution, including central Europe, the Iberian peninsula, Iceland, southeast Greenland, Labrador, western North America, and Alaska. Owing to profound changes of climate, in the transition from one geological age to another, *Zelkowa* was apparently unable to survive, except in the two restricted and widely separated areas where it is now found.

122. Continuous Distribution.—Continuous distribution is of two types: *ubiquitous*, like the bracken fern, and *isolated*, like the redwoods, *Sequoia*. In the latter case two suppositions are possible: either the species or genus is very new and has not had time to spread (*indigenous endemic*); or it is very old and a relict endemic, as defined above. Which of these two alternatives is correct for any given case may be ascertained only on the basis of comparative anatomic evidence, or on fossil evidence, or on both.

The motile sperms and the structure of the wood of the maiden-hair tree (*Ginkgo biloba*), for example, point without question to affinities with an older type of seed-bearing plants, the Cycads. In the case of the genus *Sequoia*, with only two living species, the coast redwood (*S. sempervirens*) and the giant redwood (*S. gigantea*), restricted in range to one state, California, the fossil evidence shows that these two species are the meager

remains (relict endemics) of a genus of several species, which, in Tertiary times, was widespread over most of the northern hemisphere (Fig. 77).

By a like balancing of evidence we are able to ascertain that the ubiquitous fern family, *Polypodiaceæ*, with some 200 genera and about 3,000 species, is a comparatively modern group, while the *Osmunda* family,

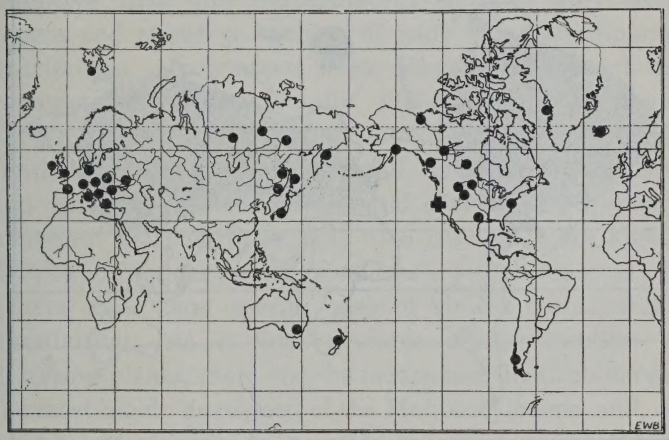


FIG. 77.—Map showing the known geographical distribution of *Sequoia* during the Cenozoic era. The cross indicates the only known location of living specimens. (After E. W. Berry.)

with only two (or possibly three) living genera and some ten species, and with wide but discontinuous distribution, is much older. The greater antiquity indicated for the Osmundaceæ by the facts of their geographical distribution is also attested by fossil evidence, and further by the nature of their spores. The spores when mature contain chlorophyll, and this fact, of itself, indicates antiquity; for this and other structural and physiological reasons,

they quickly perish unless they find at once suitable conditions for germination and development. Thus they could not spread rapidly over large areas. In the light of these facts the only logical inference is that their wide and discontinuous distribution must have required a vast period of time. The tulip tree, represented now by only one genus (*Liriodendron*) and one or possibly

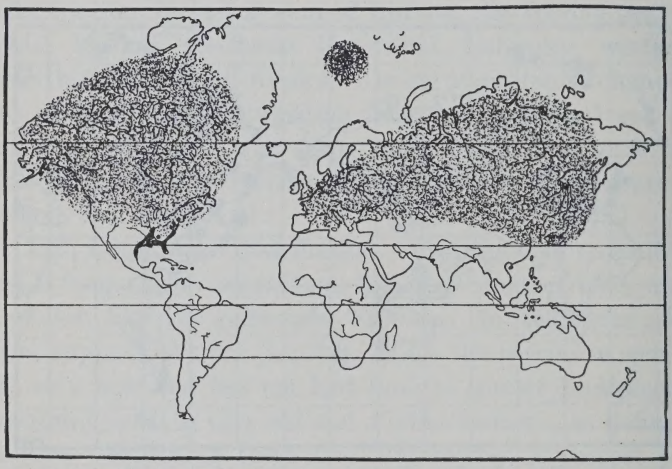


FIG. 78.—Map showing the known geographical distribution of the bald cypress (*Taxodium*) in the Tertiary and Pleistocene. Tertiary distribution, shaded; Pleistocene occurrences north of its present limits, in dots; present distribution, black. (From Shimer, after E. W. Berry.)

two species, and with discontinuous distribution (Eastern North America and China), represents an old type now, perhaps, on the way to extinction. A similar statement may be made for *Sassafras*, for the bald cypress (*Taxodium*, Fig. 78), and numerous other groups.

In general it may be said that groups considered relatively more primitive or ancient on morphological or paleonto-

logical grounds, are characterized by few genera and a restricted or (if wide) discontinuous distribution. Thus the Barberry family, one of the relatively primitive groups of dicotyledons, contains only about 10 genera and over 130 species, found in temperate North America and Asia, temperate South America, and sparingly in the tropics; the Nymphæaceæ (Water lily family), more primitive than the Berberidaceæ, contains only eight genera and about 50 species, of wide but discontinuous distribution. In contrast there may be mentioned the gamopetalous Potato family (Solanaceæ), with about 70 genera and 1,600 species, found generally on every continent, and in New Zealand, Hawaii, Australasia, and other oceanic and continental islands, and specially abundant in the tropics; and also the still more highly developed Madder family (*Rubiaceæ*), with as many as 355 genera and 5,500 species, also of almost cosmopolitan distribution. As a final example among families of flowering plants, there may be mentioned the Orchidaceæ, the most highly developed of the Monocotyledons, and, on morphological grounds, possibly the most recent family of seed-bearing plants. This family contains about 430 genera and over 5,000 species, of almost cosmopolitan distribution, most abundant in the tropics, and gradually diminishing toward the poles. The seeds of orchids are very tiny, and the embryo consists of a few undifferentiated cells. They are capable of rapid and wide distribution (Fig. 78*a*).

In the Nympheaceæ is the relatively primitive genus, *Nelumbo*, containing only two species, one the lotus (*N. lutea*), in North America, the other the Oriental lotus (*N. nucifera*), in Asia and Australasia. In the

Rubiaceæ is the genus *Mitchella*, also relatively primitive, and containing only two species, one in Japan, the other the Partridge berry (*M. repens*) in North America.

123. Evidence from the Distribution of Liverworts.—The geographical distribution of the lower cryptogams (below the ferns and their allies) has not been the subject of as extensive study as that of the ferns and flowering plants, but the evidence marshalled by Campbell[1] in 1907, concerning the distribution of the liverworts (*Hepaticæ*), illustrates in a striking manner the importance of the

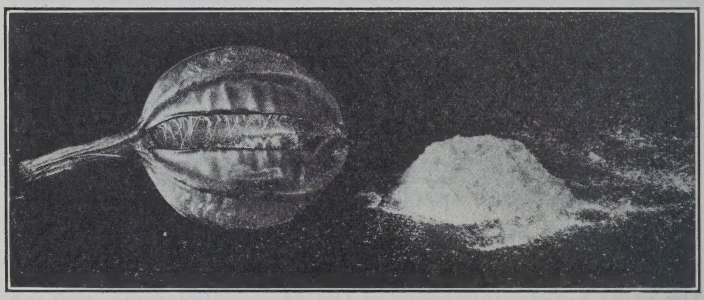


FIG. 78*a*.—Seed capsule and seeds of an orchid.

facts of geographical distribution in endeavoring to determine the question of the relative age of a group of plants. It had been argued by Scott, in 1906, that the liverworts were probably of comparatively recent origin because of the almost entire absence of fossil remains in the Paleozoic rocks. But, as Scott himself records, impressions have been described from Paleozoic strata of plant forms that can be assigned only to the Hepaticæ, and indeed to one of the most highly organized groups—the

[1] Campbell, Douglas Houghton. On the distribution of the Hepaticæ, and its significance. *New Phytologist* **6**: 203–212. Oct. 1907.

Marchantiaceæ. This, of course, means a long period of evolutionary development from similar forms to the more complex, preceding the geological age of the rocks containing the fossil record, and one such bit of positive evidence fully substantiated, is of itself sufficient to establish the antiquity of the liverworts. Moreover, when such testimony is in agreement with the evidence derived from other sources, such as comparative morphology and geographical distribution, the fact of antiquity would seem to be reasonably well established. Now, in addition to the evidence of comparative morphology, there are, as Campbell points out, certain facts of distribution that can only be satisfactorily interpreted on the basis of the comparative antiquity of the liverworts.[1] The liverworts are a widely distributed group; some of the genera are *cosmopolitan*, *i.e.*, they are found practically everywhere, in all continents, climates, and habitats, and widely on oceanic islands. *Riccia* and *Marchantia* are cosmopolitan genera of continuous distribution. Other genera are of wide, but discontinuous distribution, such, for example, as *Targionia*, a genus containing only two species, which are found in Southern and Western Europe, Africa, Java, Australia, and Western America, but are absent from Eastern America and from most of Asia. The familiar *Lunularia cruciata* of our greenhouses has a distribution similar to *Targionia* in the eastern hemisphere, but is unknown in the western hemisphere except where introduced.

[1] Throughout the discussion of liverworts I have drawn freely on Campbell's article, cited above, and have, to a certain extent, adopted his wording, asking the reader and the author quoted to accept this statement in lieu of frequent quotes.

A third type of distribution is that of limited range, such as has been mentioned above for the venus's fly-trap and the giant redwood trees. Among genera thus distributed are *Wiesnerella Javanica* Schiff., known at present only from Mt. Gedeh, in Java, and *Geothallus tuberosus* Campbell, known only from near San Diego, California. These ranges may ultimately be extended, as was that of *Treubia insignis*, known for a time only from Mt. Gedeh, but later found by its original discoverer in New Zealand.

As already noted, in order to become widely distributed, either continuously or discontinuously, a plant must either

1. Have reproductive bodies capable of rapid distribution over wide areas, or

2. Possess sufficient antiquity to have been in process of dissemination for a comparatively long period of time. In the former case, its reproductive bodies must be of such nature as to resist unfavorable environment and vicissitudes, during transit over long distances, and be able to establish themselves readily in the new habitat, especially in competition with the plants already established, and possibly also in an unfavorable environment. Now the spores of many of the most widely distributed *Hepaticæ* are not of this nature. We can hardly explain the present distribution of such widespread tropical genera as *Dendroceros*, *Monoclea*, and *Dumortiera*, says Campbell, by the theory that their spores could be carried across the wide ocean barriers that separate the regions where they now occur, as the spores are not of the type that could be carried long distances without perishing. Since there are no connecting forms in the higher latitudes that could explain the passage of these forms from one tropical zone to the other, we can

only assume that these genera are the little changed descendants of ancient, widely distributed types.

Although making a special search for Liverworts on Krakatoa in 1906, Campbell found no specimens, nor up to that time had any other collector. Professor Treub, of the Botanic Garden at Buitenzorg, Java, had reported two species of mosses. "Inasmuch as Krakatoa is within sight of Java and Sumatra, both of which have an extremely rich hepatic flora, the absence of these plants from the new flora of Krakatoa is, to say the least, worthy of note." In a similar way Campbell argues that the wide distribution of mosses (cosmopolitan in the case of the genus Sphagnum), combined with the inability of their reproductive bodies to withstand transportation over great distances, indicates a great antiquity for the group; and this inference is substantiated by the meager but positive evidence of fossil remains.

In a later discussion of the origin of the Hawaiian flora, Campbell[1] notes that the filmy ferns, since they are hydrophytic with a rain-forest habit, and are, therefore, not suited to transportation over wide stretches of ocean, must have existed in Hawaii since those islands were connected with some mainland, now submerged. The relatively shallow water between Hawaii and the Australasian-Malaysian regions, as compared to the great depths between Hawaii and North America, indicate a former mainland connection to the west, and this inference is further substantiated by the great preponderance of Australasian-Malaysian plants in Hawaii over those represented in America. In this connection

[1] Campbell, D. H. The origin of the Hawaiian flora. *Mem. Torrey Bot. Club*, **17**: 90–96. June, 1918.

is should be noted that a considerable proportion of the species of the strand vegetation of Hawaii are endemic, but many of the introduced littorals are known to be transported by ocean currents from the north Pacific.[1]

124. Distribution of Algæ.—And finally, to bring all the great phyla under brief review, it may be mentioned that facts of distribution of the Algæ point to a great antiquity for the group. This is not only in harmony with the generally accepted evidence from comparative morphology, but is substantiated by fossil remains, in early Paleozoic rocks, of calcareous Siphonogamous forms related to living calcareous forms. The absence of fossil remains of non-calcareous green forms is readily explained by the delicate nature of their tissues.

125. Hypothesis of "Age and Area."—As noted above (p. 165), an endemic species is one found in a given locality but not elsewhere. According to some botanists[2] endemism is a criterion of youth. The area occupied by a species *within a given country*, argues Willis, varies directly with its age *within that country*; that is, the longer it has been a part of the flora, the wider the area it occupies, *so long as conditions remain constant.* But Willis enumerates various conditions that would interfere with the operation of this law, including "chance" (*i.e.*, causes not understood), the action of man (clearing of forests,[3] etc.),

[1] Twenty-one littorals and eleven pseudo-littorals, out of a total of over 75, are listed as endemic by Vaughan MacCaughey. *Bull. Torrey Bot. Club*, **45**: 259–277. July, 1918.

[2] Willis, J. C. The relative age of endemic species and other controversial points. *Ann. Bot.* **31**: 189–208. April, 1917. James Small (see p. 148) has characterized Willis's Age and Area hypothesis, as the most important contribution to geographical botany since the *Origin of Species*.

[3] *Macrozamia Moorei* is being systematically exterminated in Australia because it is poisonous to cattle.

interposition of barriers (mountains, broad deserts, salt water areas, sudden changes of climate from one district to the next, geological changes, natural selection, local adaptation (the possession of a character useful in one country but not in another), the dying out of occasional old species, the arrival of a migrating species at its climate limit, et cetera. But on the whole the endemic species, says Willis, are the youngest. As an illustration of the operation of the hypothesis of age and area, Small (*l.c.*, p. 25–30) mentions numerous Compositæ which have limited distribution, although there would seem to be practically no limit to the distance their pappose seeds can be transported by wind. They are limited (endemic) *because* they are young.

According to another view,[1] endemic species are the oldest species of a region; they are either *relicts*, and thus very ancient, or they represent types which have been in the region so long that their original characters have been lost. The latter are *indigenes*, and are spoken of as *indigenous* to the country. Endemics, according to Sinnott, contain a greater percentage of trees than do *wides* (or *polydemics*)[2] but, according to the same author, trees and shrubs are older than herbs, and therefore the endemic woody species must be older than the herbaceous element of a given flora. The hypothesis of Willis demands that herbs be considered as an older form of vegetation than trees and shrubs, which, others argue, is contrary to a mass of evidence. Trees are more common as endemics (in Ceylon, *e.g.*, twice as common), notwithstanding the fact that they spread less rapidly than herbs. After its

[1] Sinnott, Edmund W. The "age and area" hypothesis and the problem of endemism. *Ann. Bot.* **31**: 209–216. April, 1917.

[2] "Wides" and "polydemics" are used as antonyms of endemics.

first rapid spread, says Sinnott, a species becomes less common the older its age of occupation.

Reviewing these two theories, Taylor[1] holds that, in the flora of the vicinity of New York at least, endemism is not a criterion of antiquity nor of youth, for while many endemics of the flora of New York and vicinity are very recent (as the hypothesis of Willis would require), and while some of them are even found in the geologically recent portion of the area (one, *Hibiscus occuliroseus*, being a salt marsh plant and therefore very 'new'), other forms are relict endemics (p. 167), and could not, therefore, be of very recent origin.[2]

As an example of relict (and therefore old) endemics (outside the local flora region of New York, there may be cited the well known case of the giant and coast redwoods (*Sequoia gigantea* and *S. sempervirens*), and the begonia, *Hilldebrandia sandwicensis*, endemic in Hawaii.[3]

An example of an indigenous (and therefore relatively recent) endemic, is the well-known insectivorous plant, Venus fly-trap (*Dionœa muscipula*), a genus having only one species, *i.e.*, monotypic (Fig. 79). This unique plant is found in sandy swamps, only in a narrow strip of country

[1] Taylor, N. Endemism in the flora of the vicinity of New York. *Torreya* **16**: 18–27. Jan. 1916.

[2] Five cases of apparently relict endemism are cited by Taylor from the vicinity of New York. *Torreya* **16** : 18-27. Jan. 1916.

[3] The Begoniaceæ have scarcely any representatives in the islands of the southern, equatorial, and Northern Pacific, but are abundant in the Andes region of South America and Mexico. The endemic begonia of Hawaii is regarded by MacCaughey (*Bot. Gaz.* **66**: 273–275. Sept. 1918) as one of several bits of evidence that "at one time in the history of the Pacific basin the Hawaiian islands were much more closely associated with the Andean and South Pacific regions than they are at present. See also p. 175.

about ten miles wide and extending about 40 miles south of Wilmington, North Carolina. The yellow waterlily (*Nymphæa mexicana* Zuccarini)[1] may also be cited as an aquatic

FIG. 79.—Venus fly trap (*Dionæa muscipula*).

example of an indigenous endemic, being known only from Florida, Texas, and Mexico.[2]

[1] *Castalia flava* Greene (1888).

[2] Conard, Henry S. The waterlilies, p. 167 and 213. Carnegie Institution of Washington, Publication No. 4. 1905.

Again, as Taylor points out, most of the recent endemics in the New York flora are not woody, the proportion of woody species among the endemics (17 per cent.) being essentially the same as for the entire flora (18.2 per cent.) Most of the endemics are probably accounted for by generic and specific instability, that is, by the tendency of existing forms to vary, at or near the edge of their range, and for the variations to become established. At least one is a case of "habitat" endemism; that is, the endemic species is confined to a given locality because suited to the environment afforded by that locality. This is illustrated by *Prunus Gravesii*, a saxitile form of the beach-plum (*P. maritima*).

Many factors are involved in the phenomena of endemism, and here, as in the case of discontinuous geographical distribution, each case must be carefully analyzed by itself. In view of our present restricted knowledge, we can generalize only with extreme caution.

126. An Illustrative Study.—As an illustration of the application of evidence from various sources in an endeavor to decide the relative age of two large groups of plants, herbs and woody plants (trees and shrubs), there may be mentioned the recent work of Sinnott and Bailey,[1] who marshalled evidence from paleobotany, anatomy, phylogeny, and phytogeography, as bearing on the relative antiquity of herbaceous and woody plants. Very briefly summarized, their argument runs as follows:

1. A study of fossil plants shows that the remains of

[1] Sinnott, Edmund W. and Irving W. Bailey. Investigations on the phylogeny of the Angiosperms: No. 4. The origin and dispersal of herbaceous Angiosperms. *Ann. Bot.* 112: 547–600. Oct. 1914. The phraseology of the authors is freely incorporated in the above very brief summary.

Angiosperms in earlier geological periods were almost all woody. The number of herbaceous forms increases as we pass from older to more recent strata. Fossils of herbaceous plants are rarely found in Cretaceous rocks but become increasingly abundant throughout the Tertiary. Caution is necessary here, however, for the foliage and other parts of herbs are more tender and delicate than those of woody plants, and therefore less liable to be preserved as fossils. This evidence is significant only in connection with evidence derived from other sources.

2. A study of the comparative anatomy of stems indicates that the continuous ring of wood, which characterizes the stems of all trees and shrubs, is a more primitive character than the separate fibro-vascular bundles of herbaceous stems. It is suggested that a change from a woody to an herbaceous type may have resulted from regional decrease in the activity of the cambium layer, from which the wood is formed by cell-division followed by lignification.

3. Evidence from phylogeny shows that the more primitive groups of Angiosperms and their probable ancestors are composed overwhelmingly of woody plants. In more than half of the families of Dicotyledons there are no herbaceous species, and the few families which are entirely herbaceous are almost all insectivorous plants, water plants, parasites, or monotypic families,[1] and hence can lay no claim to great antiquity. Also, there is a much larger proportion of woody plants in the lower groups of Angiosperms (Apetalæ and Polypetalæ) than in the higher groups (Sympetalæ.)

4. From a study of plant geography we learn that

[1] *A monotypic family* is a family having only one genus.

dicotyledonous herbs preponderate in north temperate regions, and woody plants in the tropics. The latter climate probably approaches more nearly to that under which Angiosperms first appeared. Herbs, having a short life cycle (one to two or three seasons) are able to survive periods of intense cold in the form of seeds, and would, therefore, survive in larger numbers than woody plants on the advance and retreat of the continental ice sheet of the Glacial period. This would account for the fact of a much smaller proportion of woody plants in the flora of Europe, for these could not migrate southward, as the ice encroached, since the mountain ranges there have a general east-west trend (in contrast to the general north-south trend of American ranges), and southern migration would necessitate an ascent to high altitudes that would be fatal to temperate or subtropical species.

The above facts are not cited as established, but only to illustrate a method. There is also evidence and argument suggesting the opposite conclusion, namely, that herbaceous plants are older than woody.

CHAPTER XI

PALEOBOTANY

127. The Scope of Paleobotany.—The study of fossil plants, though of course a phase of botany, constitutes a science by itself, not only covering a special subject matter, but having its own methods (technique), and possessing a large literature. It is called paleobotany. One cannot pursue this study without a knowledge of the anatomy and morphology of living forms. This is necessary in order to interpret the meaning of plant fossils, which often occur only in small fragments of the entire plant. Moreover, one must have a good knowledge of at least the elements of geology, since fossils are found in rocks. One must not only know the geological age to which the fossil-bearing rock he studies belongs, but also something of the geological processes by which fossils, and even the rocks themselves, are formed.

128. What is a Fossil?—A fossil is any remains of a plant or animal that lived in a geological age preceding the present; these remains are preserved in rocks.[1] There are two methods of preservation, namely, *incrustation* and *petrifaction*. Incrustations are merely impressions or

[1] By an extension of the term we also speak of fossil footprints of animals, fossil ripple marks, *et cetera*. The word fossil is derivcd from the Latin *fodere* (to dig), and originally signified anything dug up.

casts resulting from the encasement of the organ or organism in the rock-forming material. The tissue itself either decayed or became carbonized, leaving only the

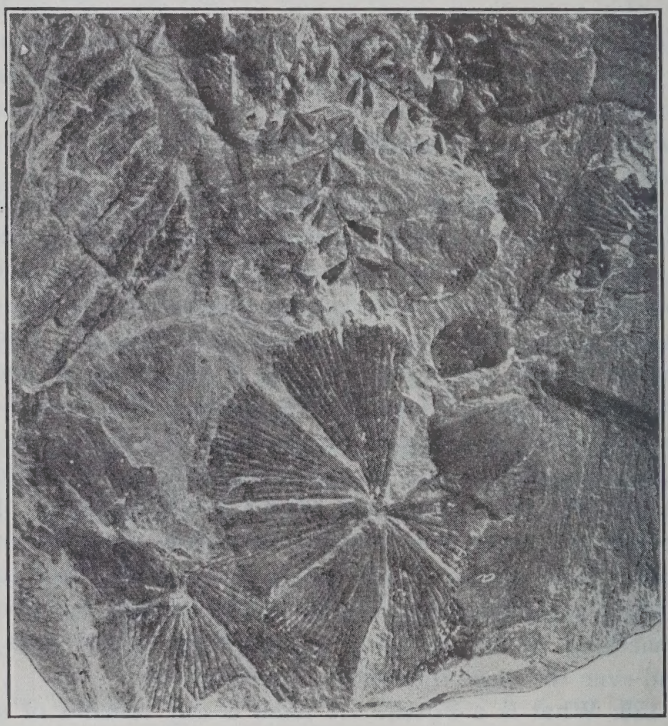


FIG. 80.—Fossil incrustations of the foliage of two species of *Sphenophyllum* from the coal measures of Missouri. (From U. S. Geological Survey.)

impression of its surface features. The well-known "fossil fern-leaves," found in coal mines, are of this nature. The tissues of the plant were transformed into coal,

leaving the impression or cast on the adjacent shale. The first stage in this process may often be observed in the autumn, when impressions of recently fallen leaves are made on the surface of wet mud. Obviously from such fossils we can learn nothing of internal structure (Fig. 80).

Petrifactions are formed by the gradual replacement of the organic tissue by mineral matter, usually carbonate of lime ($CaCO_3$) or silicic acid (H_4SiO_4). In this process the tissues become soaked with a saturated solution of the given mineral, which is gradually deposited from solution, and takes the place of the original organic matter. By this means the most minute details of microscopic structure are preserved, even in some cases the nuclei and other cell-contents (Figs. 97 and 100).

129. Conditions of Fossil-formation.—In order to understand how fossils come to be formed, we must picture to ourselves certain geological processes now in operation—the initial stages of rock-formation. Rocks are of two kinds, *igneous* and *sedimentary*. Igneous rocks result from the cooling of molten lava poured out on the surface or injected into crevices by volcanic action. Such rocks never contain fossils, as the intense heat necessary to melt the rock destroys all trace of organic matter.

Sedimentary rocks are formed by the deposit under water of the sediment formed by weathering and erosion and transported by streams. This deposit may occur along the flood-plains or at the mouths of streams emptying into inland lakes or into the ocean. In addition to rock-sediment eroded from the surface of the land, streams also transport quantities of plant (and animal) frag-

FIG. 81.—Bean Pond, near Wanakena, an extreme type of Adirondack bog. The lifeless, open-water zone, the dwarf heath-shrub, and the surrounding dwarfed black spruce are shown. At the pond margin, borings show over twenty-four feet of brown peat. This becomes shallower toward the margins of the basin, being about eight feet deep under the black spruce, one hundred yards to right of pond in the figure. (Photo by H. P. Baker. Legend quoted from W. L. Bray.) (*Cf.* Fig. 82.)

ments, leaves, stems, pieces of bark, fruit, flowers, pollen and spores, roots, and even entire plants. These natur-

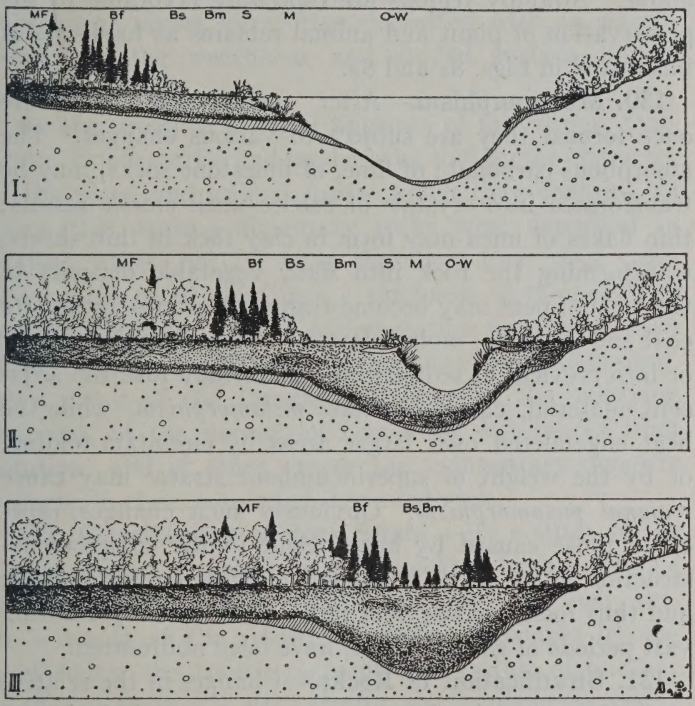


FIG. 82.—Diagram illustrating the gradual filling up of lakes by the encroachment of vegetation, and also the stages in the origin of peat and marl deposits in lakes. The several plant associations of the Bog series, displacing one another, belong to the following major groups: (1) O. W., open water succession; (2) *M.*, marginal succession; (3) *S.*, shore succession; (4) *B.*, bog succession, comprising the bog-meadow (*Bm*), bog-shrub (*Bs*) and bog-forest (*Bf*); and (5) *M. F.*, mesophytic forest succession (*Cf.* Fig. 81.) (After Bray.)

ally become buried in the mud and sediment wherever deposition takes place, and when the deposit becomes

converted into rock the organic remains may become converted into fossils by either of the processes described above. Swampy regions are especially favorable to the preservation of plant and animal remains as fossils, as is illustrated in Figs. 81 and 82.

130. Metamorphism.—After sedimentary rocks are once formed they are subject to various changes. The amorphous carbonate of lime, of limestone rocks, may be transformed into crystals of calcite until *marble* results; thin flakes of mica may form in clay rock in thin sheets, transforming the rock into *slate;* vegetable deposits in the form of peat may become transformed into anthracite coal and graphite; molten lava poured out on the surface or into crevices of sedimentary rocks may fuse the adjacent material, causing *contact metamorphism;* while the heat engendered over larger areas by mountain folding, or by the weight of superincumbent strata[1] may cause *regional metamorphism.* Obviously such changes, especially those caused by heat, result in the complete destruction of all plant or animal remains or impressions, and thus fossil records over large areas, and representing vast periods of geologic time, have been obliterated.

131. Stratification of Rocks.—Changes in the relative level of sea and land have occurred many times in the geological past, so that submerged areas of sedimentation in one period have become areas of dry land, undergoing erosion in another; and *vice versa,* areas of erosion have become areas of sedimentation. As a result of this, rocks occur in layers,[2] the deeper lying layers (with ex-

[1] Some rocks are buried under more than 40,000 feet of strata, and the temperature increases approximately 1°F. for every 50 to 60 feet of depth.

[2] Several layers form *a stratum,* or *bed.*

ceptions readily explained by geologists) being older than those above, or nearer the surface. Moreover, as a result of a second submersion following elevation and erosion, subsequent layers were often deposited with an *unconformity* on the weathered and eroded surface underneath.

By the presence of fossil imprints of rain drops, footprints, ripple marks, and mud cracks, and by the character of the plant and animal fossils which they contain, we know that most sedimentary rocks were deposited in shallow water, not far from the shore line. But since these same rocks may have a thickness of thousands of feet we know the area of sedimentation must have been slowly sinking while the sediment was being deposited. As a result of the enormous pressure of the overlying material, of the deposit of cementing substances from solution, and of other causes, the sedimentary deposits became, in time, converted into solid rock.

132. Classification of Rock Strata.—By a study of the fossils which the rocks contain, geologists have been able to classify the various strata according to their age. As a result of the period of erosion, indicated by unconformity, the transition from the stratum of one age to that of another is often abrupt, the fossils in successive periods being quite characteristic of the given stratum or period. In other cases, as for example between the Silurian and Devonian in New York State, there is no unconformity, and this renders it more difficult to decide just where the plane of division lies. The names and order of occurrence of the known rock strata are given in the following table, the older rocks being at the bottom, the most recently formed at the top.

TABLE II.—TABLE OF GEOLOGICAL TIME

Era		Period
Cenozoic	Quaternary	Holocene (recent, or the present)
		Pleistocene (ice age)
	Tertiary	Pliocene
		Miocene
		Oligocene
		Eocene
Mesozoic	Secondary	Upper Cretaceous
		Lower Cretaceous (Comanchean)
		Jurassic
		Triassic
Paleozoic	Primary	Permian
		Upper Carboniferous (Pennsylvanian)
		Lower Carboniferous (Mississippian)
		Devonian
		Silurian
		Ordovician
		Cambrian
Archean		Huronian
		Laurentian

133. Paleogeography.—By changes in the relative level of the land and sea, above referred to, rocks containing fossils may be elevated as dry land, and frequently as mountains, so that remains of marine organisms, as well as of others, are often found at high elevations. In some cases forests near the seashore have been submerged. and covered over with sediment, then elevated again as dry land, so that subsequent excavations have revealed the fossilized trunks and stumps (Figs. 83 and 84). Thus

FIG. 83.—Fossil tree stumps in a carboniferous forest, Victoria Park, Glasgow. (*Cf.* Fig. 84.) (After Seward.)

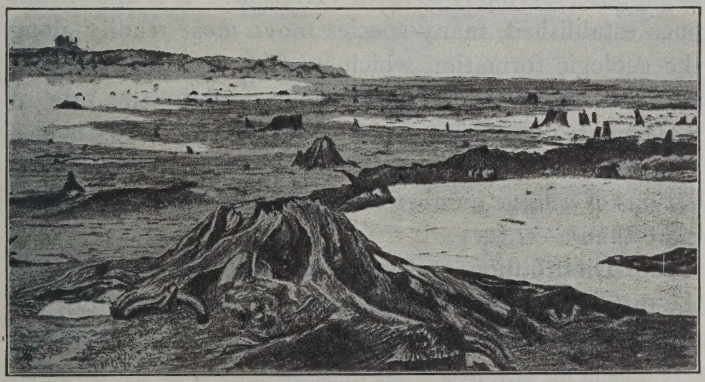


FIG. 84.—Part of a submerged forest as seen at low tide on the Cheshire coast of England. (*Cf.* Fig. 83.) (After Seward.)

it is seen that, by a study of fossils, we may not only learn of their structure and thus fill in many of the gaps in the evolutionary sequence left by a study of forms now living, but we may also learn of the distribution of plants and animals in previous geological ages—in other words, we have the basis for a science of fossil geography or *paleogeography*.

134. Plant Migrations.—With the development of Paleogeography, a clearer conception of the location and changes of the continental areas of the past is gradually being gained. As a consequence, plant geography is a subject of increasing interest to the paleobotanist. Moreover, geology, the fossil record, and the present zonal grouping of plants indicate that, in the past, the polar areas, then much warmer than now, must have been fruitful in new species.[1] High mountains or plateaus are also suggested as homes of plastic races.[2] In the tropics environments are more nearly static, and, it is reasonable to suppose, less likely to favor variation. It is knownthat once established, many species move most readily along the geologic formation which supplies the exact soil constituents most favorable to their growth, the rate of movement often being rapid. Flotation of seeds is also a factor. The facts here briefly cited rest on the observations of a large number of investigators, extending over more than a century.

135. Distribution of Plants in Time.—In addition to the distribution of plants in space (plant geography), the problem of their distribution in geologic time is one of

[1] Owing to the precession of the equinoxes these areas undergo an extreme variation in the length of winter and summer of 37 days every, 12,934 years.

[2] *Cf.* pp. 148–149.

absorbing interest and importance. The following table indicates the known distribution of the various plant groups from the earliest geologic time to the present.

TABLE III.—DISTRIBUTION OF PLANTS IN GEOLOGIC TIME[1]

Division	Subdivision, class, or order	Range	Common name or example
IV. Spermatophyta Cycadophyta — Angiospermæ	Monocotyledones	Comanchean to present	Oaks
	Dicotyledones	Comanchean to present	Grasses
IV. Spermatophyta Cycadophyta — Gymnospermæ	Gnetales	(Fossil record scant)	Ephedra
	Coniferales	Permian to present	Pines
	Ginkgoales	Permian to present	Ginkgo
	Cordaitales	Devonian to Jurassic	Cordaites
	Cycadales	Permian to present	Cycads
	Cycadofilicales	Devonian to Comanchian	Neuropteris
III Lepidophyta	Lycopodiales	Devonian to present	Club mosses
III Calamophyta	Equisitales	Devonian to present	Horsetails
III	Sphenophyllales	Devonian to Permian	Sphenophyllum
III Pteridophyta	Filicales	Devonian to present	Ferns
II. Bryophyta	Musci	Tertiary to present	Mosses
	Hepaticæ	Tertiary[2] to present	Liverworts
I. Thallophyta	Fungi	Silurian to present	Fungi
	Algæ	Pre-Cambrian to present	Seaweeds
	Diatomeæ	Jurassic to present	Diatoms
	Schizophyta	Pennsylvanian to present	Bacteria
	Myxomycetæ	(Fossil record lacking)	Slime-molds

[1] Modified from Shimer. [2] See, however, p. 172.

136. Gaps in the Fossil Record.—In the *Origin of Species* Darwin called attention to the paltry display of fossils in our museums, as evidence of how little we really know of the plant and animal life of past ages. "The number, both of specimens and of species, preserved in

our museums," says Darwin, "is absolutely as nothing compared with the number of generations which must have passed away during a single formation." The meagerness of the record is, of course, due in part to the relatively small area explored in proportion to the whole; but there are other reasons much more serious, because they represent opportunities lost forever. Among them are metamorphosis, explained above, and the fact that many of the organisms of the past were composed wholly or largely of soft tissues, which were entirely destroyed, by decay or otherwise, in the process of rock-formation. Such plants, for example, as *Spirogyra* and many other algæ, the fleshy fungi, and, among animals, jelly-fish, earthworms, and others, would form fossils only under exceptionally favorable circumstances, if at all.

But there is an even more effective cause of obliteration of the fossil record in the long-continued erosion and denudation represented by unconformity in the rock strata. In many cases only a small proportion now remains of the thickness of a rock stratum originally deposited, and all traces of the plant and animal life that may have existed on the denuded area have thus been obliterated forever. These blank intervals between successive periods were of vast duration.

"I look at the geological record," said Darwin, "as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly changing language, more or less different in the successive chapters, may

represent the forms of life, which are entombed in our consecutive formations, and which falsely appear to have been abruptly introduced."[1] These views have received added emphasis from the recent development of Paleogeography.

137. Factors of Extinction.—The question may naturally arise, "Why did the species common in previous geological ages die out, giving place to newer forms?" The answer is found in the facts of struggle for existence and survival of the fittest. In the words of the great American botanist, Asa Gray, species may continue only "while the external conditions of their being or well-being continue." The struggle may be with other organisms or with the physical conditions of the environment. Among the more important factors of extinction, may be mentioned the following:

1. *Struggle with Other Plants for Adequate Space.*—This is illustrated in a simple way by the crowding out of cultivated plants by weeds in a neglected garden, or of grass by dandelions or chickweed in a lawn. By more rapid germination and growth, and by other "weedy" characteristics, the weeds get the start of the cultivated plants, occupying all available space, and choking them out.

2. *Attacks of disease-causing parasites, e.g.,* chestnut trees by a parasitic fungus, elm tress by the elm tree beetle.

3. *Changes of Environment too Great or too Rapid to Permit of Readjustment.*—Plants are plastic organisms, and can adapt or readjust themselves to considerable environmental change, but there are limits of speed and amount of change beyond which readjustment is not possible, and the plant must consequently perish. If such changes

[1] Darwin, C. "Origin of Species," vol. 2, p. 88. New York, 1902.

involve the entire area of distribution of the species concerned, the species will, obviously, become extinct. The following nine factors (paragraphs 4–12) are specific instances of this.

4. *Diminished Water Supply.*—Aquatic plants may be destroyed by the draining of a pond or lake; hydrophytic forms by the drying up of a swamp. Sometimes forms suited to conditions of moderate water supply (*hydrophytes*) are destroyd by the conversion of wide areas into desert regions, as has doubtless occurred. If such changes are gradual, resting spores (*e.g.*, *Spirogyra*), winter buds (*e.g.*, *Utricularia*, *Elodea*, *Vallisneria*), and seeds readily transported by wind (*e.g.*, cat-tail) enable the species to become reëstablished in a new location, but not so when the changes are too abrupt, or cover too wide an area.

5. *Temperature changes*, when too abrupt, too extreme, or too long continued. When the continental ice-sheet advanced southward during the glacial period, many forms, adapted only to temperate conditions, became extinct. Fossils of extinct tropical plants are found in Greenland, which is now undergoing a glacial period.

6. *Volcanic eruptions*, such, for example, as those of Mount Pelée, which occurred in 1902, on the island of Martinique, W. I., often destroy all signs of life over a radius of many miles. In the states of Washington, Oregon, and Idaho floods of molten lava, covering thousands of square miles, have, during a previous geological age, been poured out over the surface, forming a wide plateau.

A great volcanic eruption in Alaska, in prehistoric times, covered an area of over 140 square miles with a deposit of ash and pumice varying in thickness from a

few inches near the margin to some 300 feet near the crater. In 1883 the eruption of Krakatoa, in the Straits of Sunda, killed practically all the plants and animals on an island of five square miles in area, and on neighboring islands; a part of the island was completely blown away, leaving only deep water. So recently as 1912 the eruption of Katmai, in Alaska, spread a layer of ash nearly a foot deep over the entire surface of Kodiak Island, one hundred miles from the volcano, and killed all the herbaceous vegetation, leaving only trees and bushes. It is almost certain that many species of plants and animals have become extinct by such agencies. Not only the lava, but poisonous gases that fiill the air during volcanic eruptions, may prove fatal to plant and animal life.

7. *Encroachment of salt water* in coastal regions, caused by changes in the level of the land, resulting in the killing of fresh-water vegetation. According to Fernald, one of the sundews, *Drosera filiformis*, is known to occur in only two regions, namely along the Gulf coast from Florida to Mississippi, and along the Atlantic coast from Maryland to Massachusetts (Fig. 85). Its extinction in the intervening region is explained by the subsidence and drowning of a former high continental shelf, along which this and other species migrated northward during the late Tertiary. If a similar subsidence should occur in the two limited regions where the species is now found it would become extinct unless, by some combination of circumstances, it could migrate and become established in new localities. It is not unlikely that species have often been exterminated in this way.

8. *Encroachment of Fresh Water over Land Areas.*— Previous to about the year 1900, the Salton basin, in

lower California, was a saline area of a so pronounced desert type that its flora contained less than 140 species of ferns and flowerng plants, five of which were endemic. During the winter of 1904–1905 the fresh waters of the Colorado River began to debouche into this basin, and by early 1907 had formed a brackish lake, over 80 feet deep and of about 450 square miles in area, known as the Salton Sea. At the end of ten years it still had an area of somewhat less than 300 square miles. Some three or four hundred years previously the entire Salton Basin was

FIG. 85.—Sketch map showing the geographical distribution of the sundew, *Drosera filiformis*. (After M. L. Fernald.)

occupied with a lake of over 2,000 square miles in area, which, in turn, had dried up and given place to the desert conditions above mentioned. It is not improbable that such drastic changes as this may have resulted in the obliteration of one or more species, though the flora was not well enough known previous to the last inundation to make a definite statement on this point possible. For example, the presence there of endemic species was not known until the recent botanical survey of the region lying between the late water level and that of the ancient

sea. According to MacDougal,[1] if the water had risen in 1907 to its ancient level of three or four hundred years ago, it would have destroyed all these endemic species.

7. *Transformation of fresh water lakes into salt lakes,* as in the case of the Caspian Sea, and the Great Salt Lake of Utah (18 per cent. salt). This change gradually exterminates plant and animal life until the given body of water becomes a true "dead" sea, where practically nothing remains alive, as in the Dead Sea (24 per cent. salt). A more extreme case yet is Lake Van, in Turkey, where saline matter constitutes over one-third of the contents. In the last stages of such transformations the lake may give place to a salt marsh or plain (*salina*). South of Lake Titicaca, in the Andes Mts. of Bolivia, ar several salinas, one of some 4000 square miles in area, with a layer of salt three or four feet thick.

10. *Disturbance of Symbiotic Relationships.*—The interrelationships of organisms are very complex, affording innumerable opportunities for extinction by a disturbance of adjustments. Shade-loving forms in a forest may perish by the destruction of those affording the shade; obligate parasites may perish from the destruction of the necessary host; plants dependent upon certain insects for cross-pollination may perish on account of the extinction of the necessary insects.

11. *Diminution of Carbon Dioxide in the Atmosphere.*—There are reasons for thinking that in certain past ages the atmosphere was richer than now in carbon dioxide, and that that condition was favorable to the development of certain vegetatively vigorous species which cannot live in an atmosphere like the present, having a smaller percentage of carbon.

[1] In a letter to the author.

12. *Denudation of the Land Surface.*—In the course of ages even lofty mountains are planed down by erosion, and the arctic and sub-arctic species of the high altitudes thus undergo extinction. Furthermore, erosion may be coupled with general subsidence. In fact, not only do geologists now recognize numerous old mountain "roots," such for example as the Adirondack region of New York State, but there are also abundant evidences of periodic emergencies and subsidence of areas of continental extent, quite throughout geologic time. The climatic and other environmental disturbances accompanying such changes would inevitably result in the extinction of certain species. (See also ¶ 129.)

CHAPTER XII

THE EVOLUTION OF PLANTS (Concluded)

138. Evidences from Fossil Plants.—The study of fossil plant remains has greatly enlarged our knowledge of the course of plant evolution, filling in gaps derived from the study of living forms, and affording new facts, not disclosed by the study of plants now living. Like the study of comparative anatomy and life histories, paleobotany teaches us that there has been a gradual evolutionary progress from the simple to the more complex, but it has also disclosed the fact that some of the complex forms are much more ancient than had been inferred from the study of living plants only.

139. Discovery of Seed-bearing Ferns.—For example, remains of seed-bearing plants, quite as highly organized as those of to-day, are found far back in the earliest fossil-bearing strata of the Paleozoic. Great forest types existed as early as the Devonian. Later in the Carboniferous occur many seed-bearing ferns. These have been called *Cycadofilicales* (cycadaceous ferns), or, by some, *Pteridosperms*. Recent studies have disclosed the fact that most of the fossil plants from the Carboniferous coal-bearing strata, formerly thought to be ferns, are not even cryptogams, but are these fern-like seed-bearing plants. The best known pteridosperm is *Lyginodendron oldhamium* (Fig. 86), first described from fossil leaves, in 1829, as a tree-fern, under the name *Sphenopteris Hoeninghausi*. After investigations extending over nearly 90 years, "we are

now in position to draw a fairly complete picture of the plant as it must have appeared when living.

"It was in effect a little tree-fern, with long, slender, sometimes branched, stem, 4 centimeters or less in diame-

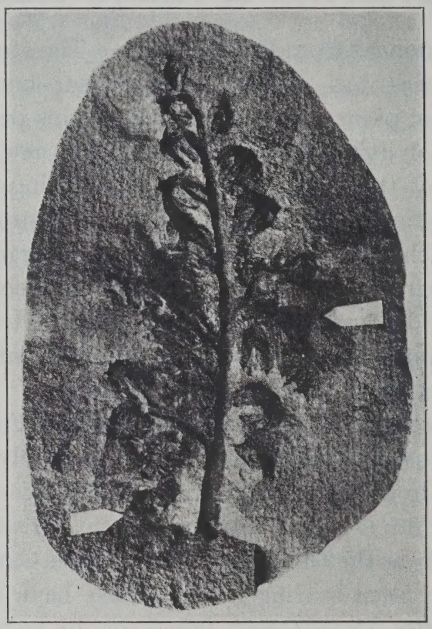


FIG. 86.—*Lyginodendron oldhamium.* Pinna of a microsporophyll, found in an ironstone nodule. Before its identity was established this specimen was named *Crossotheca Hoeninghausi.* The somewhat peltate fertile pinules on the ultimate branches, bear each a fringe of microsporangia about 3 mm. long. The appearance has been likened to that of a fringed epaulet. (After Scott, from a photo by Kidston.)

ter, and provided with spines by means of which it probably climbed on its neighbors. The foliage was disposed spirally and consisted of relatively very large, finely divided fronds with small, thick pinnules with revolute

margins, suggesting a xerophytic or halophytic habitat. The stem in the lower portion gave rise to numbers of slender roots, some of which appear to have been aerial in their origin. These grew downward and often branched where they entered the soil.

FIG. 87.—Young leaf of the Cycad, *Bowenia serrulata*. Comparison of this with a leaf of the fern *Angiopteris* (Fig. 88) shows how difficult it might be to decide from a fossil leaf whether the plant was a cycad or a fern. (*Cf.*, also, Fig. 91.) (Photo from specimen in Brooklyn Botanic Garden.)

"The stems, roots, and petioles, and even the pinnules, have been found calcified and so beautifully preserved that their entire structure can be made out with certainty. Without going into a technical description of these organs, it may be said that the stem when young, and before secondary growth has begun, has a very strong resemblance

to the stem of [the fern] *Osmunda*, but when more mature certain cycadean characters appear to predominate."[1]

Its foliage and other characters closely resemble some of our modern tree-ferns (*Cf.* Figs. 87 and 88), but more

FIG. 88.—Leaf of a fern (*Angiopteris evecta*). (*Cf.* Fig. 87.)

careful study of the calcified specimens of much beauty, found in calcareous nodules (the so-called English "coal balls"[2]), has disclosed both the microsporophylls,

[1] Knowlton, F. H. *American Fern Journal*, **5**:85. 1915.

[2] Coal balls are "concretions of the carbonates of lime and magnesia which formed around certain masses of the peaty vegetation as centers and, through inclosing and interpenetrating them, preserved them from the peculiar processes of decay which converted the rest of the vegetation into coal. In them the mineral matter slowly replaced the vegetable matter, molecule by molecule, thus preserving the cellular structure to a remarkable degree. Such balls are especially frequent in the coal of certain parts of England (Lancashire and Yorkshire)." Shimer, H. W. "*An introduction to the study of fossils*," p. 53. London, 1914.

bearing pollen-sacs, and the megasporophylls, bearing, not merely megasporangia, but *true seeds*. The ovule has a *pollen-chamber*, like the cycads, except that it projects a bit through the micropyle, and, strange as it may seem, fossil pollen-grains have been discovered, well preserved within this chamber. The seeds, about ¼ inch long, have been described as resembling little acorns, enclosed like hazelnuts in smaller glandular cupules (Fig. 89). They are similar to those of the cycads, except that they are not known to have organized an embryo with cotyle-

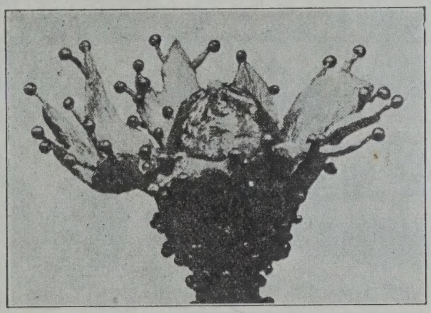


FIG. 89.—Restoration of a seed of *Lyginodendron oldhamium* (*Lagenostema Lomaxi*), from a model by H. E. Smedley. (After Scott.)

dons and caulicle. Instead, the tissues of the female gametophyte only are so far found, retained within the megasporangium, which is enclosed in the integument. In this connection it is of interest to note that the seeds of some modern plants (*e.g.*, orchids) do not possess differentiated embryos, but whether this is a primitive or a reduced character is not certain. The pollen was formed in spindle-shaped pollen-sacs, having two chambers, and borne in clusters of four to six on the under side of little oval discs, from 2 to 3 millimeters long. These structures

are found on pinnules of ordinary foliage leaves, resembling the sporophylls of certain ferns (Fig. 90) rather than the stamens of modern flowers.

The discovery of the seed-bearing character of the fern-like plants of the Paleozoic has been called the most important contribution of paleobotany to botany ever made. It was predicted by Wieland, of Yale University, nearly two years before it was announced by Oliver and Scott. It is now believed that seed-bearing plants of the pterido-

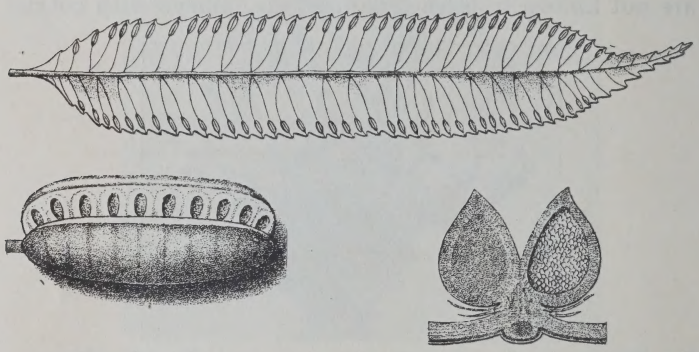


FIG. 90.—Top, lateral pinna from a leaf of *Marattia fraxinea*. (After Bitter.) Below at left, synangium of same. (After Bitter.) At right, cross-section of the synangium. (After Hooker-Baker.)

sperm type were nearly as numerous in the Paleozoic as were the cryptogams.

140. Significance of the "Pteridosperms."—The close resemblance of the pteridosperms to ferns, on the one hand, and to modern cycads on the other, justifies the conclusion that they represent a "connecting link" between the true ferns and the cycads, and that the modern cycads have descended from the same ancestry as the modern ferns, each developing along somewhat different lines.

It was in recognition of their vegetative resemblances that the Pteridosperms were first called (by Potonié) Cycadofilices, now *Cycadofilicales*. Van Tieghem tersely described them as "phanerogams without flowers."

141. A Modern Fern-like Cycad.—One of the modern cycads (*Stangeria paradoxa*)[1] is of much interest in this

FIG. 91.—*Stangeria paradoxa* Moore. Specimen from the cycad house at the New York Botanical Garden, bearing, at the apex of the stem a carpellate cone. (Photo from New York Botanical Garden.)

connection. So closely does it resemble a certain fern (*Lomaria*) that the botanist Kunze, who first described it when it was brought from Natal to the botanic garden at Chelsea, England, supposed it was a fern, and named it *Lomaria eriopus*. The specimen possessed no fruit, which would have helped to identify it. Its leaves, with circinate

[1] *Stangeria paradoxa* Moore = *Stangeria eriopus* (Kunze) Nash.

vernation, have a pinnately compound blade, and leaflets with pinnate dichotomous venation. Two or three years later another botanist, examining it more closely, pronounced it a "fern-like Zamia or a Zamia-like fern." These facts show how puzzling the specimen was, and how

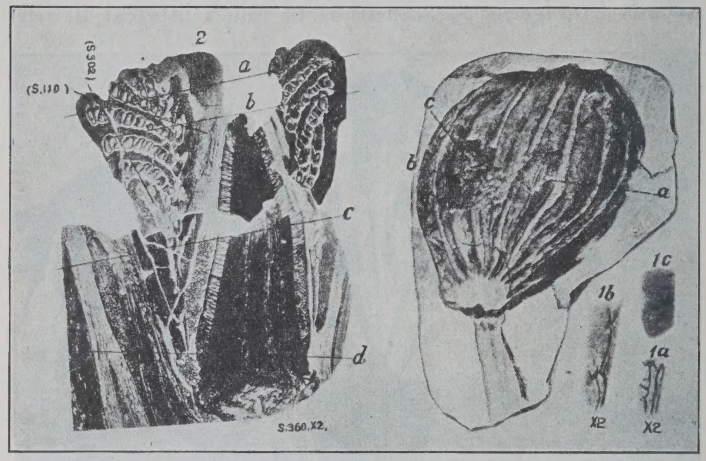


FIG. 92.—To the left, *Cacadeoidea dacotensis* Macbride. Longitudinal section of a silicified specimen of a bisporangiate cone (unexpanded flower), so taken that the pinnules of the microsporophylls on both sides of the central axis, or receptacle, are successively cut throughout their entire length. The lines indicate the planes of various sections through the cone, published in Wieland's "American Fossil Cycads." To the right *Cycadocephalus Sewardi* Nathorst. Microsporangiate cone, natural size, preserved as an impression on a flat slab. From a fossil-bearing bed of the Trias, at Bjuf, Southern Sweden. (Left figure from Wieland, right figure from Nathorst.)

closely a plant may resemble both a cycadophyte and a fern. In a sense this plant may be called a living fossil. Specimens have since come into flower in botanic gardens, and the typical cycadaceous cones (Fig. 91) leave no doubt that the plant is a true cycadophyte.

142. Derivation of New Types.—Attention should here again be called to the fact that the theory of evolution does not teach that one given species becomes transformed into another, but simply that new species are descended from older forms which may or may not continue to exist. It is not supposed, for example, that ferns developed into

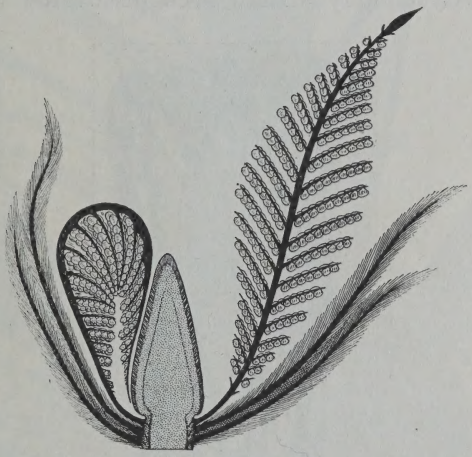


FIG. 93.—*Cycadeoidea dacotensis*. Semi-diagrammatic sketch of a flower (bisporangiate cone), cut longitudinally; one sporophyll folded, and one (at the right) arbitrarily expanded. At the center is the apical, cone-shaped receptacle, invested by a zone of short-stalked ovules and interseminal scales. The pinnules of the sporophylls bear the compound sporangia (*Synangia*). Exterior to the flower are several hairy bracts. About three-fourths natural size. (After Wieland.)

cycads, and cycads into higher gymnosperms, but that there has been an unbroken line of descent (possibly more than one) in the plant kingdom, that closely related forms (like ferns and cycads) have descended from a common ancestral type which may or may not now be found. We must not, in other words, expect necessarily to find in

fossil forms the direct ancestors of those now living, although a study of their structure is of the greatest value in enabling us to understand the genetic relationships of the great groups of plants.

143. Ancestors of the Angiosperms.—Just as the Cycadofilicales indicate the ancestry of the cycads, so fossil types of Cycadophyta have been discovered which are

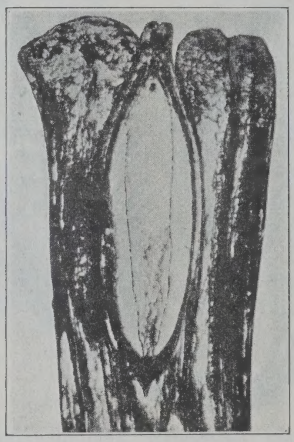


FIG. 94.—*Cycadeoidea dacotensis* (?). Photomicrograph of a young seed (× 15), showing a sterile scale on either side. Between them projects the entire length of the tube through which the micropyle extends. The partially collapsed nucellus is distinctly shown in the center. (After Wieland.)

interpreted by some paleobotanists as ancestors of the modern angiosperms. Other investigators, however, dissent from this view and consider that we have not yet sufficient knowledge of fossil forms to be justified in designating the ancestors of the Angiosperms. This difference of opinion is largely due to the meagerness of the available evidence. As one writer has stated it, "A

trayful of flowers may be all the record of the Pteridosperms from the Devonian on. The gaps in the evidence are always enormous."

Although the Cycadophyta are now a very insignificant element in the earth's flora, in the Mesozoic period

FIG. 95.—*Macrozamia spiralis*. Tip of the trunk, showing three *lateral* cones, inserted in the axils of leaves. Photo from specimen in Brooklyn Botanic Garden. (*Cf.* Fig. 96.)

they form about one-third of the recovered vegetation of the land. One order, the Hemicycadales (Bennettitales[1]), then had a cosmopolitan distribution and seemingly was as important as the Dicotyledons are now. Over 30 species of the petrified stems have been found in the Mesozoic

[1] In his paper on the *Classification of the Cycadophyta* (Am. Jour. Sci. **47**: 391–406. June, 1919), Wieland states "simple and good reasons" for letting the name Bennettitales fall into disuse, and substituting therefore the term Hemicycadales (half-cycads).

terrains of the United States, the Black Hills of South Dakota alone yielding a score. The Isle of Portland forms

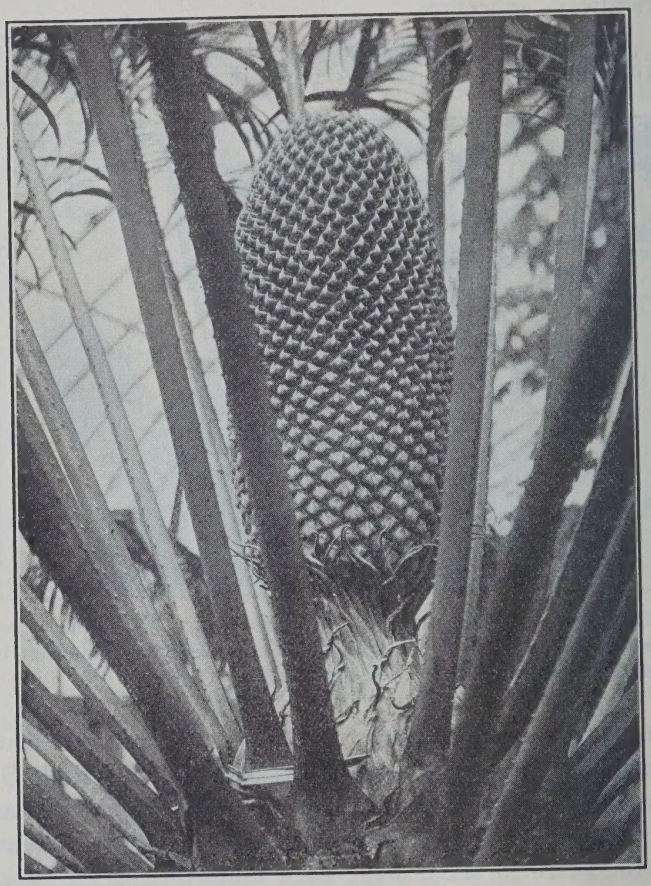


FIG. 96.—*Cycas circinalis.* Tip of trunk, showing numerous leaf-stalks, and the large *terminal* cone. Photo from specimen in Brooklyn Botanic Garden. (*Cf.* Fig. 95.)

were called *Cycadeoidea* by the celebrated geologist Buckland. The original name of the order was derived from

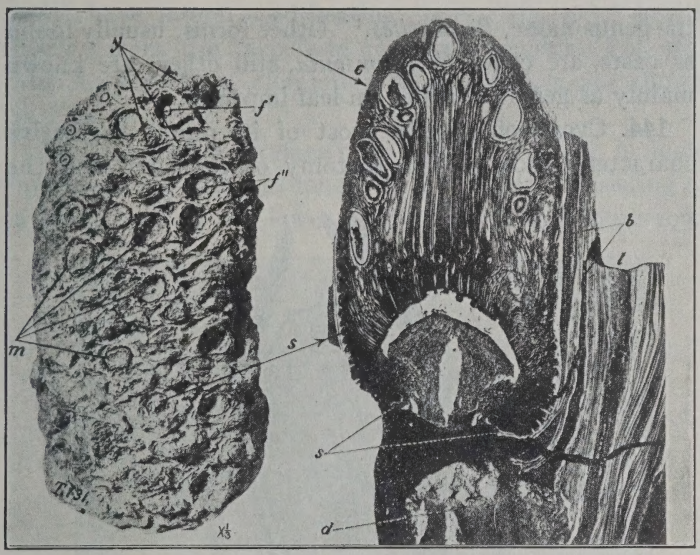


FIG. 97.—*Cycadeoidea Wielandi.* At left, a finely preserved trunk bearing many ovulate cones with seeds approaching maturity, and a lesser number of either young or abortive cones. *f'*, Receptacle of a shed or non-preserved cone with surrounding bracts yet present; *f''*, two cones broken away during erosion, with a portion of the basal infertile pedicel yet remaining; *m*, four cones eroded down to the surface of the armor, in this instance about or a little beneath the level of the lowermost seeds; *y*, three of the dozen or more very young cones, in some cases known to be simply ovulate and to be regarded as having aborted or else as belonging to a later and sparser series of fructifications than the seed-bearing cones present, the latter unquestionably representing the culminant fruit-producing period in the life of this cycad; *s* (over lower arrow), the ovulate strobilus, shown at the right, in its natural position, this photograph having been made before the cone was cut out by a cylindrical drill. × 0.5.

At right, longitudinal section of the small ovulate strobilus cut from its natural position on the trunk as denoted by the arrow *s*, in photograph 1. *c* (upper arrow), seed with dicotyledonous embryo preserved, cotyledons being similarly present in the lowermost seed on the left-hand side of the strobilus; *s*, traces of hypogynous staminate disk; *b*, bracts; *l*, leaf bases. × 5. (After Wieland.)

the genus-name, *Bennettites*.[1] Other forms, usually found as casts, are called *Williamsonia*, still others are known mainly as genera founded on leaf imprints.

144. Cycadeoidea.—In most of its purely vegetative characters, such as the anatomy of the stem and the

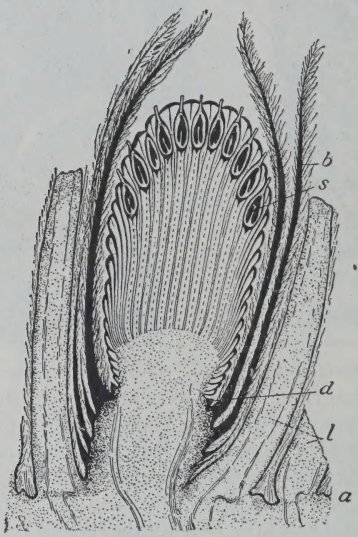


FIG. 98.—*Cycadeoidea Wielandi*. Longitudinal section through the axis of a female inflorescence, or cone. *l*, old leaf-base; *d*, insertion of disc; *s*, erect seed, borne at summit of seed-pedicle inserted on convex receptacle; *b*, hair-covered bract. (After Wieland.)

structure of the leaves, *Cycadeoidea* resembled modern cycads, but its reproductive branches were characteristically lateral, which is one of the most fundamental characteristics of the higher seed-bearing plants of today. Only two modern cycads (*Macrozamia* and *Bow-*

[1] *Cycadeoidea* Buckland = *Bennettites* Carruthers.

enia) have lateral seed-bearing cones (Fig. 95);[1] in the other genera the carpellate cones are terminal (Fig. 96). Various structural characters of *Cycadeoidea* are shown in Figs. 92–100.

In *Cycadeoidea dacotensis* the "flower," which in some specimens was 5 inches long, was a strobilus, consisting of a thick axis on the lower part of which were numerous

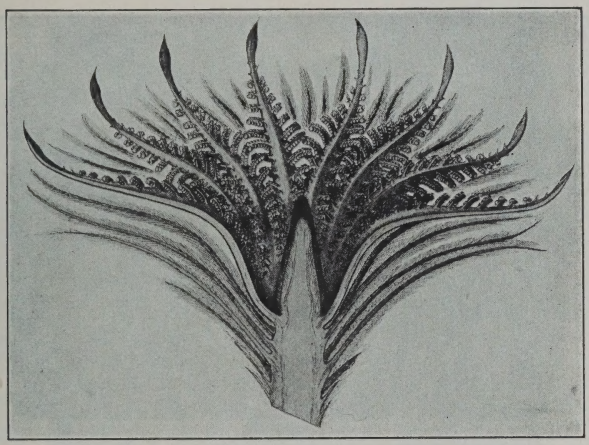


FIG. 99.—*Cycadeoidea ingens*. Restoration of an expanded bisporangiate cone, or flower, in nearly longitudinal section. Restored from a silicified fossil. (After Wieland.)

bracts arranged in spirals. The bracts surrounded a *campanula* of about 20 stamens. Each stamen was, in reality, a pinnately compound sporophyll, about 4 inches long, rolled in toward the center of the flower, and bearing two rows of compound microsporangia (pollen-sacs) on each leaflet. They thus closely resembled the sporophyll of a fern.

[1] The staminate cones of *Zamia* are lateral.

The axis of the flower terminated in a cone-shaped receptacle, bearing the stalked ovules, and numerous sterile scales (Figs. 97 and 98). The mature seeds often contain the well-preserved fossil embryos, with *two cotyledons* which quite fill out the nucellus, and show that there was little or *no endosperm.* These are characters never found in the lowest group of modern seed-

FIG. 100.—*Cycadeoidea Dartoni.* Tangential section through outer tissues of the (fossilized) trunk, showing the very numerous seed-cones. The seeds are very small (the illustration being natural size), and nearly every one has a dicotyledonous embryo. There were over 500 such cones on the original stem. (After a photograph loaned by Prof. Wieland.)

bearing plants (the Gymnosperms), but only in the highest group of Angiosperms, the Dicotyledons. In fact, the French paleobotanist, Saporta, called some of the Cycadeoids, *Proangiosperms.*

145. Relation of Cycadeoidea to Modern Angiosperms. —The question of the ancestry of the Angiosperms is the most important problem of paleobotany. Although the

Hemicycadales possess many of the primitive anatomical features that characterize the Cycadofilicales, their development of a bisporangiate strobilus with two sets of sporophylls, related to one another as they are in the flower of the Angiosperms, indicates a genetic relationship to that group, as does also the fact that the seeds, enclosed in a fruit, possess a dicotyledonous embryo, without endo-

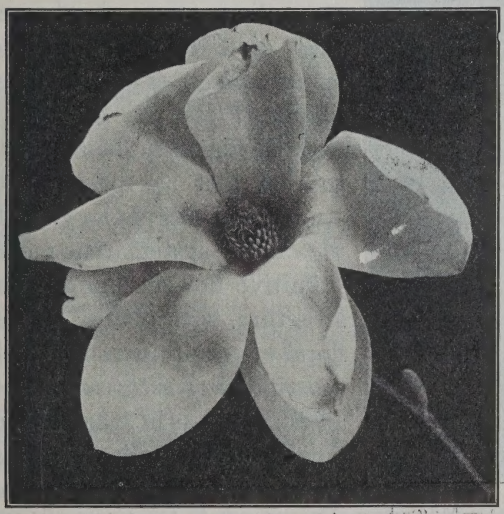


FIG. 101.—Flower of magnolia. (*Cf.* Fig. 102.)

sperm. In other features the Hemicycadales are unlike the Angiosperms; the ovules, for example, are enclosed by sterile scales, instead of by the carpels on which they are borne, and the protrusion of the pollen-chamber through the micropyle signifies the gymnospermous type of fertilization.

These and other comparisons indicate that the Hemicycadales were essentially Gymnosperms having certain

Angiospermous characters, and therefore, while they are not to be considered as the ancestors of the Angiosperms, it is probable that they and the modern dicotyledons are both descended from a common branch of the ancestral tree. Among modern plants, the flower of the magnolias most closely resembles that of *Cycadeoidea* in the spiral arrangement of its stamens and pistils (Figs. 101 and 102). Just what significance should be attached to that fact has been disputed by students of morphology. The older view of the systematists regarded the primitive flower as more complex in structure, with pistils, stamens, and floral envelopes arranged spirally in centripetal or *acropetal* succession on a fleshy axis, as in *Magnolia* and other flowers of the order *Ranales;* other types of floral structure were considered as derived from this one by reduction. This is often referred to as the "Strobiloid theory of the flower" (*Cf.* pp. 132 and 134).

FIG. 102.—Magnolia. Flower with perianth removed, showing the compound pistil, and four of the stamens. Most of the stamens have been removed so as to bring out their spiral arrangement as shown by the scars at the points of attachment. (*Cf.* Fig. 101.)

A more recent view recognizes that simple staminate or pistillate flowers may, *in some cases*, be interpreted as derived by reduction from more complex forms, but regards the primitive flower as uni-

sexual—in effect a microsporophyll or a megasporophyll, from which complex forms were derived by elaboration. This latter view, however, is not in harmony with available evidence from fossil plants, such as that afforded by *Cycadeoidea*.

"The strobiloid theory of the flower seems in the present state of our knowledge to stand alone as a working hy-

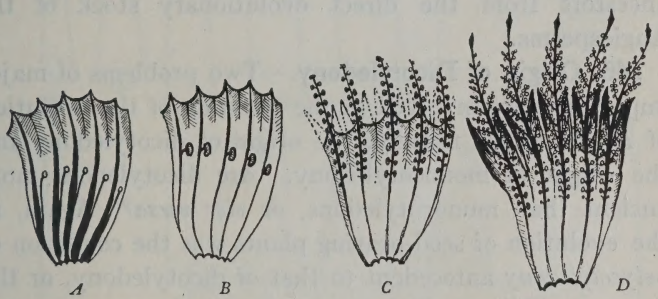


FIG. 103.—Theoretical stages in the reduction (from *Cycadeoidea* to modern Angiosperms) of staminate discs represented as segments. *A*, any common campanulate form with simple stamens (*e.g.*, morning glory); *B*, hypothetical Cycadeoid reduced to a single synangium to each frond component; *C*, inner view of a sector of a *Williamsonia mexicana* disc; *D*, sector of a *Cycadeoidea dacotensis* disc with the pair of shoulder spurs borne by each frond. (After Wieland.)

pothesis. If we reject it, we are left without any historical clue to the origin of the floral structure of Angiosperms. If we accept it, the Primitive Angiosperm must be credited with a flower resembling that of *Magnolia* or *Liriodendron* in general plan."[1] From this it follows that the *Magnoliaceæ* must be among the most primitive, if not the most primitive, of all Angiosperms, as Wieland first and Hallier later and independently pointed out.

[1] Sargant, Ethel. The reconstruction of a race of primitive Angiosperms. *Ann. Bot.* **22**:121–186. April, 1908.

The gap between the stamen of *Cycadeoidea* and the type characteristic of modern Angiosperms is partially bridged by the genus *Williamsonia* (which has simple *vs.* pinnately compound stamens), and by another genus, *Wielandiella*, both older genera than *Cycadeoidea* (Fig. 103). From this it has been inferred that the Hemicycadales are a lateral branch, further removed than their ancestors from the direct evolutionary stock of the Angiosperms.

146. Origin of Dicotyledony.—Two problems of major importance are involved in the question of the evolution of Angiosperms, namely, the origin of dicotyledony and the origin of monocotyledony. Are dicotyledons more ancient than monocotyledons, or *vice versa?* Again, in the evolution of seed-bearing plants was the condition of *polycotyledony* antecedent to that of dicotyledony, or the reverse? This would be a comparatively easy question to answer if we had an unbroken series of fossil remains of the primitive and intermediate spermatophytes; but unfortunately such evidence has not yet been discovered. We know nothing of the embryos of the geological ancestors of modern conifers. The Mesozoic gymnosperms (*Cycadeoidea* and other related genera) are known to have had dicotyledonous embryos, but these forms do not stand in the ancestral line of the (polycotyledonous) conifers of to-day. To answer our question, therefore, we must, for the present, depend largely on the study of living forms. The evidence has seemed conflicting, and for nearly three-quarters of a century opinion has varied. Adanson and Jussieu, in the early nineteenth century, contended that polycotyledony was derived from dicotyledony by a splitting of the primordia of two original cotyledons; Sachs

(1875) held the opposite opinion. Hill and de Fraine (1908–1910) are among the recent protagonists for the hypothesis that dicotyledons are the more primitive. One of the most recent studies is that by Bucholz[1] who ex-

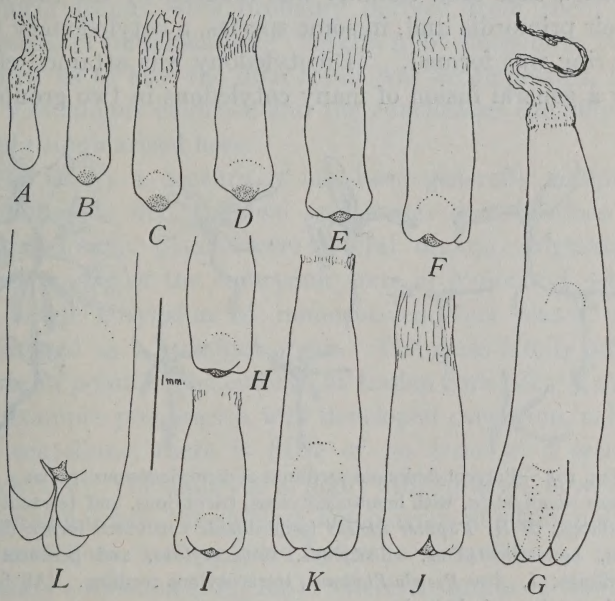


FIG. 104.—Development of stem tip and cotyledons in *Pinus Banksiana*. Dotted line represents plerome of root-tip; shaded area, meristem of stem tip; *H*, *I*, *J*, *K*, fusing cotyledons. (After Bucholz.)

amined the embryos of pine, spruce, larch, juniper, balsam fir, cedar of Lebanon, and others. Many instances of the fusion of the primordia of cotyledons were found, but no evidence of cotyledonary splitting. This fusion has resulted in reducing the number of cotyledons, and, in

[1] Bucholz, John T. Studies concerning the evolutionary status of polycotyledony. *Am. Journ. Bot.* 6 : 106–119. March, 1919.

certain species, in the formation of a *cotyledonary ring*, or tube. Bucholz interprets the facts set forth by himself and other investigators as leading to the conclusion that the more primitive gymnosperms had numerous cotyledons, that their number was reduced by the fusions of their primordia and, in some species, a cotyledonary tube or ring was formed. "Dicotyledony was attained either by a general fusion of many cotyledons in two groups, or

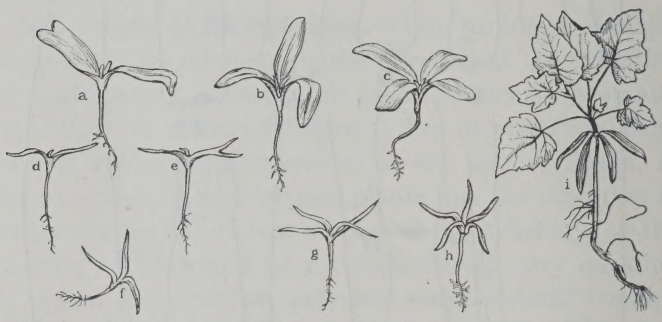


Fig. 105.—Polycotyledonous seedlings of dicotyledonous species. *A–C*, *Silene odontipetala*, with hemi-tricotylous, tricotylous, and tetracotylous seedlings; *D–H*, *Papaver Rhoeas* (semi-double cultivated form), dicotylous, hemi-tricotylous, tricotylous, tetracotylous, and pentacotylous seedlings; *I*, *Acer Pseudo-Platanus*, tetracotylous seedling. (All figures re-drawn from de Vries.)

by an extremely bilabiate development of a cotyledonary tube" (Fig. 104).

The final conclusion of Bucholz, based on the evidence of comparative anatomy, supplemented by studies of development, is that the polycotyledonous condition is the more primitive, and the dicotyledonous one derived. On the basis of this theory, the rather common abnormal appearance of supernumerary cotyledons in dicotyledonous

seeds is to be interpreted as a reversion to a more primitive condition (Fig. 105).[1]

147. Origin of Monocotyledony.—If the earliest Angiosperms were dicotyledons, as now seems probable, the monocotyledons were probably derived from them by a process of simplification. Several hypotheses have been framed as to how the final result was accomplished, but the voluminous evidence and the conclusions can only be briefly summarized here.

For nearly a century it has been generally accepted by botanists that the two seed-leaves or cotyledons of dicotyledonous plants were lateral organs, originating below the tip of the embryonic stem or hypocotyl, while the single cotyledon of monocotyledonous plants was considered as a terminal organ. The grass family offers a case in point. The embryo of Indian corn (*Zea Mays*), for example possesses a well developed cotyledon, called the scutellum; there is little or no trace of a second cotyledon. The embryos of many other grasses, however, possess an organ, the *epiblast*, homologous in position with the scutellum, and regarded by earlier botanists as a rudimentary cotyledon (Fig. 106). Recent studies of Coulter and Land leave little doubt of this as the correct interpretation of that organ.

A study by Bruns (1882) of 82 genera of grasses, repre-

[1] According to de Vries (The Mutation theory. 2: 393–456. Chicago, 1910) tricotylous intermediate races do not arise by selection but by mutation, tricotyly being the expression of an ancestral character which is *latent* in the normal species. If the normal character is active and the anomaly *semi-latent* we have what de Vries calls a "half-race;" if the normal character becomes latent and the anomaly active, we have a "constant variety." Sometimes an equilibrium is maintained in the expression of the normal character and the anomaly, giving rise to a "middle race," or "eversporting variety."

senting 12 tribes, demonstrated the presence of the rudimentary cotyledon (epiblast) in 29 of the genera, repre-

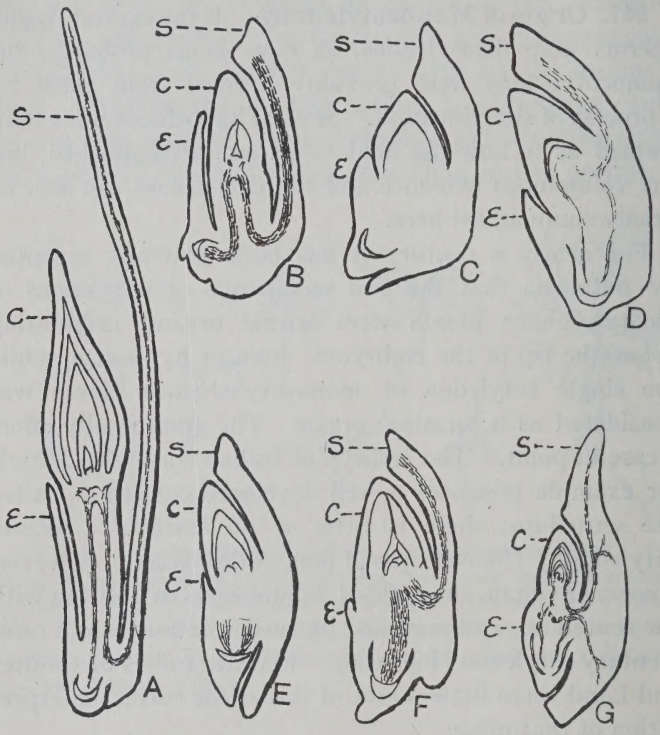


FIG. 106.—Diagram of longitudinal sections of grass-embryos (Gramineæ) to illustrate the rudimentary cotyledon (*epiblast*). *A–C*, *E–G*, redrawn from J. M. Coulter, after Bruns; *D*, from nature. *A*, *Zizania aquatica; B*, *Leersia clandestina; C*, *Leptochloa arabica; D*, *Triticum vulgare; E*, *Spartina cynosuroides; F*, *Triticum vulgare; G*, *Zea Mays; s*, scutellum; *c*, coleoptile; *e*, epiblast.

senting nine tribes; later studies by Van Tieghem (1897) disclosed the presence of an epiblast in 61 out of 91 genera examined. From these figures we may reasonably infer

that the majority of the so-called "monocotyledonous" grasses possess two cotyledons, one of which is more or less rudimentary, and that the grasses are primitive monocotyledons, representing a transitional stage from dicotyledons to the higher monocotyledons. Monocotyledony, then, as stated by Coulter, is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony by reduction, and involving no abrupt transfer of a lateral organ to a terminal origin. Variations in the relative size of the second cotyledon in grass embyros are illustrated in Fig 106.

Henslow[1] was among the first to suggest the origin of monocotyledons from dicotyledons.[2] Previous to the publication of his paper, it was generally assumed that monocotyledons were the older group, and Henslow stated that no systematist of his day recognized any real points of connection between the two groups. He proposed the hypothesis that the monocotyledons were derived by the arrest of the development of one seed-leaf in a primitive dicotyledonous Angiosperm;[3] hence said Henslow, "only one elongates, its superior vigour carrying it on in a straight

[1] Henslow, Rev. George. A theoretical origin of endogens from exogens, through self-adaptation to an aquatic habit. *Journ. Linnean Soc. Bot.* **19**: 485–528. May 15, 1893.

[2] The first to make the suggestion appears to have been Agardh, in his *Lärobok i Botanik*, Part I. Malinö, 1829–32.

[3] In discussing the origin of Angiosperms, Arber (*Journ. Linnean Soc. Bot.* **38**: 29–80. July, 1907) calls attention to the "Law of corresponding stages in evolution," namely, that in the evolution of seed-plants, the stages reached by different organs at any one period are dissimilar. From this law it follows that such a plant as a "primitive Angiosperm," in the strict sense of the term, that is, with all its organs primitive, never existed in reality. We must picture the ancestors of modern Angiosperms as having certain organs in a primitive stage of evolutionary development, others as more advanced toward the stage in which they are now found.

line with the suspensor, finally making the cotyledon terminal." This he calls "the real interpretation of a monocotyledonous embryo." Henslow further inferred a very early origin of monocotyledons from dicotyledons, from the fact that so many of their orders contain very few genera and monotypic groups, for groups of plants or animals with few members, are regarded, in general, as survivals, representing a lost ancestry. He recorded voluminous observations in support of his theory, and, among other evidence, called attention to "Dicotyledonous monocotyledons" such as *Tamus communis* (black bryony), a tuberous rhizomed species of the Yam family, where the first foliage leaf, situated exactly opposite the cotyledon, is interpreted (with Dutrochet) as a second cotyledon; and to "Monocotyledonous dicotyledons," especially among aquatic species such as the water-chestnut (*Trapa natans*), where one cotyledon is arrested in its development. Other illustrations, not mentioned by Henslow, include such forms as *Dioscorea bonariensis* and *Pinguicula vulgaris* (Fig. 107). *Ranunculus Ficaria* is not an aquatic, but it flourishes by the waterside, and is regarded by Henslow as descended from an aquatic form. About one-third of the orders of of monocotyledons are aquatic, as compared to only 4 per cent. in dicotyledons, and the monocotyledonous dicotyledons are all aquatic. The final conclusion of Henslow is, "that endogens [monocotyledons] have in the first place descended from very early types of exogens [dicotyledons] . . . ; and that, secondly, the more immediate cause of their origin was an aquatic habit of life assumed by certain primitive exogenous plants."

Miss Ethel Sargant has more recently elaborated the hypothesis of the derivation of monocotyledons from

dicotyledons, by a fusion of the two cotyledons into one.[1] On this basis the single seed-leaf of monocotyledons is interpreted as homologous to the *two* seed-leaves of dicotyledons. The evidence supporting this suggestion is derived largely from a study of the anatomy of monocotyledonous seedlings. "The young epicotyl of monocotyledonous seedlings contains a single ring of collateral bundles which may even show traces of cambium, much resembling

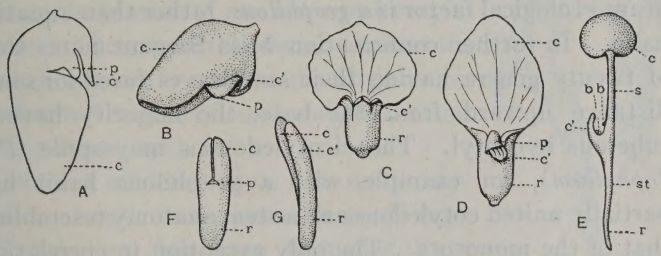


FIG. 107.—*A–B*, embryos of a "dicotyledonous monocotyledon," *A*, longitudinal section through an embryo of *Tamus communis; B, Tamus communis*, entire (*A* and *B* enlarged after Solms-Laubach.). *C–G*, embryos of "monocotyledonus dicotyledons;" *C, D, Dioscorea bonariensis*, enlarged (after Beccari); *E, Trapa natans*, the water chestnut × ½ (after Barnéoud); *F, Pinguicula vulgaris; G, Pinguicula caudata.* (*F* and *G* after Dickson, both greatly enlarged.)

dicotyledons." Professor Jeffrey has also called attention to evidence that the anatomy of the stem of the hypothetical ancestor of the Angiosperms was exogenous (dicotyledonous).

Miss Sargant has further pointed out that the few dicotyledons which possess but one seed-leaf (pseudomonocots) are widely distributed through the dicotyledonous families, from Ranunculaceæ to Umbelliferæ,

[1] *Annals of Botany* **17**: 1–88. Jan., 1903; *Botanical Gazette* **37**: 325–345. May, 1904, and other papers.

Primulaceæ, and Nyctaginaceæ, which indicates that the abnormality was not derived by inheritance from a common ancestor; its explanation, therefore, must be sought in the influence of environment. Professor Henslow, as noted above, associated the monocotyledonous tendency with an aquatic habit of life, but Miss Sargant points out that all the pseudo-monocots possess some underground organ which is thickened as a tuber, suggesting that the significant ecological factor is a *geophilous*, rather than aquatic, habit. In further confirmation Miss Sargant notes that of twenty genera having their seed-leaves fused for some distance upward from the base, the majority have a tuberous hyocotyl. The dicotyledonous may-apple (*Podophyllum*), for example, with a geophilous habit has partially united cotyledons and a stem anatomy resembling that of the monocots. The only exception to correlation of this nature is the mangrove (*Rhizophora Mangle*), a tropical tree whose seeds germinate in the air while still in the fruit.

The monocotyledons are separated from the dicotyledons by seven characters as follows:[1]

1. A single cotyledon.
2. Stem-anatomy.
3. Development of the embryo.
4. Parallel venation of leaves.
5. Short duration of primary root.
6. Seeds with endosperm.
7. Parts of the flower in threes.

Of these characters, "four have been shown to appear frequently among geophytes, and to be useful to the plant growing under conditions which determine the geophilous

[1] As enumerated by Miss Sargant.

habit. They are therefore in all probability adaptations to that habit. Two more—stem anatomy and the apparently terminal cotyledon in the embryo—may be considered as direct consequences of such adaptations; the stem anatomy acquiring its peculiar features from the insertions of numerous broad-based leaves on a squat subterranean axis, and the embryonic cotyledonary number arising from the congenital fusion of two ancestral cotyledons. The seventh character—trimerous floral symmetry—bears no obvious relation to the geophilous habit, but is not inconsistent with it."

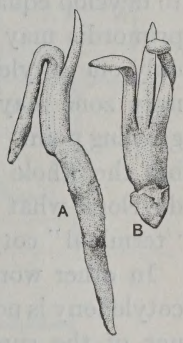


FIG. 108.—*Agapanthus umbellatus*. *A*, monocotyledonous embryo. *B*, dicotyledonous embryo. (Redrawn from photo by W. J. G. Land.)

Recent evidence as to how monocotyledony may have been derived from dicotyledony has been furnished by a study of the embryogeny of *Agapanthus umbellatus* L'Her (Fig. 108), a South African plant of the Lily family.

The sequence of events is as follows.[1] As the massive pro-embryo enlarges the root-end elongates, thus remaining narrow and pointed; while the shoot-end widens, becoming relatively broad and flattish. At this broad and flat end the peripheral cells remain in a state of more active division than do the central cells, and form what is known as the *cotyledonary zone*. In this zone two more active points (*primordia*) appear and begin to develop. Soon the whole zone is involved in more rapid growth, resulting in a ring or

[1] The above description closely follows Coulter and Land. The origin of monocotyledony. *Bot. Gaz.* **57**: 509–518. June, 1914.

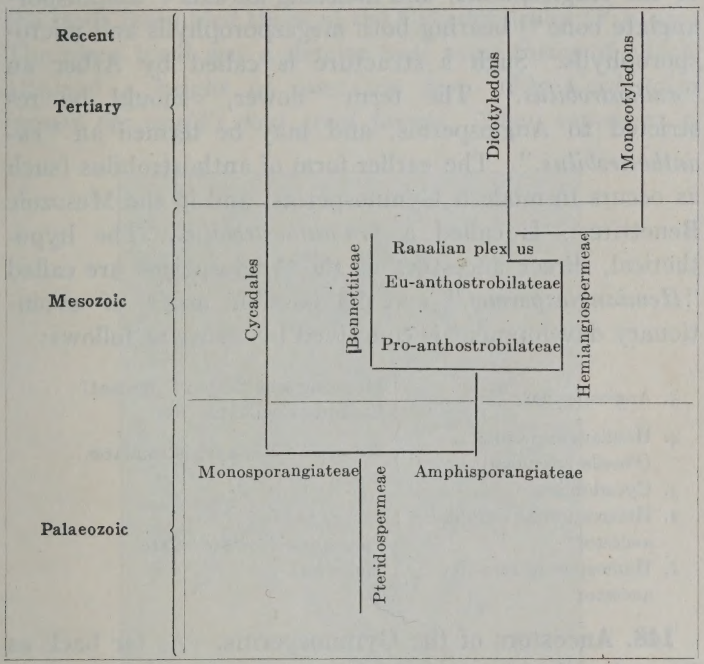
tube, but with the primordia still evident. The cotyledonary zone continues its growth until a tube of considerable length is developed, leaving the apex of the proembryo depressed. At this stage either one of two things may occur. As the cotyledonary zone continues to grow, the two primordia on the rim of the tube may continue to develop equally, forming two cotyledons; or one of the primordia may cease to grow, resulting in an embryo of only one cotyledon; in other words, the entire cotyledonary zone may develop under the guidance of only one growing point. It is not that one cotyledon is eliminated, but the whole growth is diverted into one. There thus develops what appears to be an "open sheath" and a "terminal" cotyledon.

In other words, according to Coulter and Land, monocotyledony is not the result of the fusion of two cotyledons, nor of the suppression of one; but is simply the continuation of one growing point on the cotyledonary ring, rather than a division of the growth between two growing points. In a similar way, polycotyledony is the appearance and continued development of more than two growing points on the cotyledonous ring (*Cf.* p. 222, and Fig. 104).

We are not in possession of enough facts to construct a genealogical tree showing the derivation of Monocotyledons from Dicotyledons, nor the derivation of the original Angiosperm stock, but the table of Arber and Parkin (Table IV, p. 231) shows in a very general provisional way a possible course of events, and the approximate geological period when the various advances were made, beginning with the Paleozoic Cycadofilices (Pteridosperms).

The first step in the immediate evolution of the Angio-

TABLE IV
(After Arber and Parkin)



sperms, according to Arber,[1] was the transfer of the pollen-collecting surface from the ovule to the carpel or carpels, resulting in the stigma as now known. "It was this act which called the Angiosperms into being."

Arber does not regard the Apetalous orders (Piperales, Amentiferous families, and Pandanales) as primitive Angiosperms, for that theory necessitates the view that the perianth arose *de novo*, by enation.[2] He considers

[1] Arber, E. A. Newell. On the origin of Angiosperms. *Jour. Linnean. Soc. Bot.* **38**: 29–80. July, 1907.

[2] *Cf.* p. 132.

the perianth an ancient structure, present in the ancestors of the Angiosperms, and inclosing an axis ("amphisporangiate cone") bearing both megasporophylls and microsporophylls. Such a structure is called by Arber an "*anthostrobilus*." The term "flower," should be restricted to Angiosperms, and may be termed an "*eu-anthostrobilus*." The earlier form of anthostrobilus (such as occurs in modern Gymnosperms, and in the Mesozoic Benettiteæ) is called a *pro-anthostrobilus*. The hypothetical, direct ancestors of the Angiosperms are called "*Hemiangiospermæ*," and the possible order of evolutionary development is conceived by Arber as follows:

5. Angiospermæ	Mesozoic and Tertiary (Recent) Eu-anthostrobilatæ.
4. Hemiangiospermæ (Fossils unknown)	Mesozoic—Pro-anthostrobilatæ.
3. Cycadofilices	
2. Heterosporous fern-like ancestor	Paleozoic—Non-strobilate ancestors.
1. Homosporous fern-like ancestor	

148. Ancestors of the Gymnosperms.—As far back as Devonian time, preceding the great coal period (Carboniferous), fossils have been found of a plant, *Cordaites* (of the order Cordaitales), common in that period, and having characters which indicate that it stands in the ancestral line of our modern conifers—that it and the conifers had a common ancestry.

The leaves of *Cordaites* resembled those of the Kauri pines (*Agathis*) of the southern hemisphere (Fig. 109), or the leaflets of *Zamia*. They varied from a decimeter to over a meter in length. The male cones resembled those of the still living *Ginkgo*, each stamen having from four

to six microsporangia (pollen-sacs) on a stalk. The female cones resembled the male in general appearance, and the seeds resembled those of the Cycadofilicales (Fig. 94). The plant itself was a slender tree, some forms of which attained a height of over 100 feet. *The Cordaitales formed the world's first great forests.* They represent a

FIG. 109.—Branch, with cones, of the Kauri pine (*Agathis australis*). (From the Gardener's Chronicle.)

wide departure from the Cryptogams, and must be considered as true seed-bearing plants. They were closely related to the *Ginkgo*—another living fossil, ranking next below the modern cone-bearing trees. We thus ascend from the ferns to the conifers by a series of transitional forms as follows (reading from the bottom, up):

6. Coniferales (modern cone-bearing trees).
5. Ginkgoales (primitive gymnosperms).
4. Cordaitales (transitional conifers).
3. Cycadales (true cycads).
2. Cycadofilicales (cycad-like ferns).
1. Filicales (true ferns).

149. Relation of the Above Groups.—It must not be inferred that the above groups were derived one from the other by descent from lower to higher. They should be interpreted rather as samples remaining to show us, not the steps, but *the kinds* of steps through which the plant kingdom has passed in developing the more highly organized, modern cone-bearing trees from more primitive forms like the ferns. As stated above, it is doubtful if the actual transitional forms have been preserved, so that the entire history of development can probably never be written.

150. A Late Paleozoic Landscape.—The frontispiece illustrates the kind of landscape that must have been common in the latter part of the Paleozoic era along sluggish streams in certain regions such as Texas and New Mexico. Of the primitive vertebrates then abounding, only a few larger types are shown. The dragon-flies of that time are known to have had a spread of wing amounting, in some cases, to as much as two feet. In the foreground, at the left, are representatives of the Cycadofilicales, some of them bushy, and others resembling our modern tree ferns. At the right are dense thickets of Calamites, the ancient representatives of our modern scouring rushes (*Equisetum*). In the background, at the left, are the unbranched, Sigillarias, and the branched Lepidodendrons. The Cordaitales, which formed the Devonian forests, were not yet extinct, but none is shown in the figure. Other forms,

ancestors of our modern conifers and angiosperms, must be imagined as hidden in the recesses of the forest.

151. Significance of the Fossil Record.—Before the brilliant discoveries in fossil botany, just outlined, were made, there had been (as stated in Chapter VI) a general tendency among botanists to consider the comparatively simple moss-plants as an older type than the fern, and that either they or their close relatives were the ancestors of Pteridophytes. As outlined in the same chapter, the sporogonium of the moss was regarded as representing the form from which, by elaboration of vegetative tissues and organs, the sporophyte of the fern was derived. This view was clearly expressed in 1884 by the noted botanist Nägeli, who considered that the sporophyte of Pteridophytes was derived from a moss-like sporogonium by the development of leafy branches.

A consideration of the fossil record, however, makes it difficult to accept this hypothesis. Not only do we find, in the fossil forms described above, sporophytes that do not bear the remotest resemblance to the moss-sporogonium, but fossil mosses and liverworts have never been positively identified in either the Palaeozoic or the Mesozoic rocks,[1] while the same rocks are rich in fossils of such advanced forms as the broad-leaved sporophytes of the Cycadofilicales and Cycadophytes. We must not, however, hastily conclude, from this lack of evidence, that mosses and liverworts did not exist in those early ages. Quite possibly they were present when the Paleozoic rocks were being deposited, though doubtless not represented by the same genera, or at least not by the same species, as are now living.

[1] *Cf.*, however, p. 172.

152. Summary of Results.—From what has been said, in this and in Chapter VI, we recognize that *the method of evolution is to be ascertained chiefly by experiment*—by studying *living plants* in action; but *the course of evolution chiefly by the study of comparative morphology, with special attention to fossil forms*, and supplemented by the facts of geographical distribution. Other points are necessary to complete the history of the evolution of plants; the above paragraphs give only the barest outline of the problem, for the entire history is much too long and much too difficult to be treated here. To summarize; the facts now known have led some investigators to infer:

1. The origin of Angiosperms from Cycadophyta (pro-angiosperms).
2. The origin of Cycadophyta from Cycadofilicales.
3. The origin of Cycadofilicales from Primofilices.[1]
4. The origin of Filicales from Primofilices.
5. The origin of Cordaitales from Primofilices.
6. The origin of Coniferales from Cordaitales.

An ancestral tree embodying these views is shown in Fig. 110.

What was the origin of the Primofilices? Here, as often in every science, we have to acknowledge that we do not know; the group is a hypothetical one, and some investigators doubt its actual existence altogether.

153. Other Views.—(*a*) Other and equally competent students of the problem take exception to one or more of the six points tabulated above. Not all of their views can here be discussed, but mention may be made of that first elaborated by Jeffrey, of Harvard University.

[1] The term *Primofilices*, not hitherto used in this text, refers to a hypothetical, primitive fern stock.

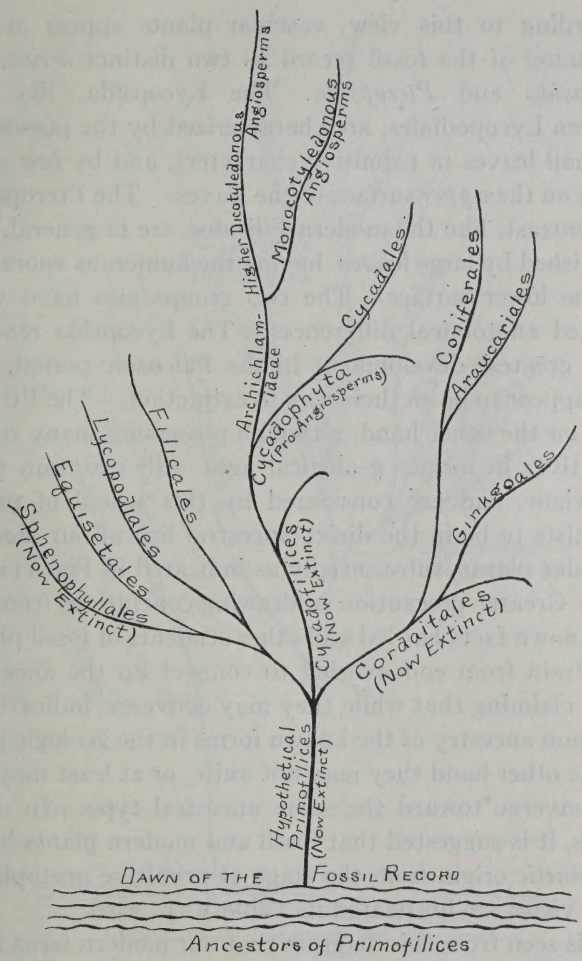


FIG. 110.—Genealogical tree, showing the ancestral lines of the modern plant orders, according to a monophyletic hypothesis. Full explanation in the text. (*Cf.* Fig. 111.)

According to this view, vascular plants appear at the beginning of the fossil record as two distinct series, the *Lycopsida* and *Pteropsida*. The Lycopsida, like the modern Lycopodiales, are characterized by the possession of small leaves (a primitive character), and by few sporangia on the *upper* surface of the leaves. The Pteropsida, by contrast, like the modern Filicales, are in general, distinguished by large leaves, having the numerous sporangia on the lower surface. The two groups also have well-marked anatomical differences. The Lycopsida reached their greatest development in the Paleozoic period, and now appear to be on their way to extinction. The Pteropsida, on the other hand, although possessing many representatives in former geological ages, still maintain their full vigor, and are considered by this school of paleobotanists to be in the direct ancestral line of our modern vascular plants, substantially as indicated in Fig. 111.[1]

(*b*) Greater precaution in drawing conclusions from the few known facts has led still other students of fossil plants to refrain from endeavoring to connect up the ancestral lines, claiming that while they may converge, indicating a common ancestry of the known forms in the geologic past, on the other hand they may not unite, or at least may not all converge toward the same ancestral type. In other words, it is suggested that fossil and modern plants had a *polygenetic* origin from the stage of primitive protoplasm. Such views are illustrated in Table V (p. 240).

It is seen from this diagram that our modern ferns have a long ancestral history, extending from the present back

[1] Scott restricts the name Lycopsida to the Lycopodiales, and proposes a third group, Sphenopsida, incuding the Equisetales, Pseudoborniales, Sphenophyllales, and Psilotales. Wieland has recently adduced reasons for using the term Hemicycadales *vs.* Bennettitales. (*Cf.* foot-note, p. 211.)

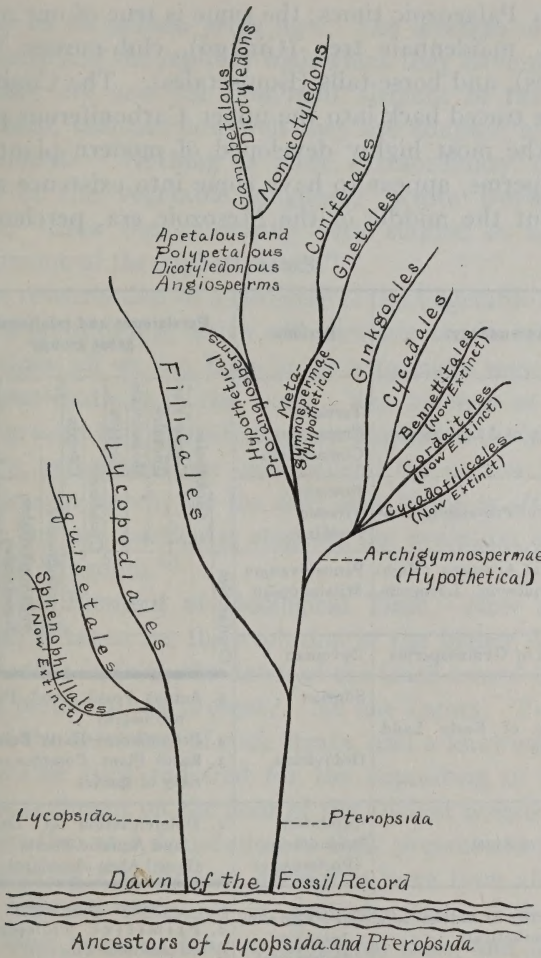


FIG. 111.—Genealogical tree, showing the ancestral line of the modern plant orders according to a polyphyletic hypothesis. Full explanation in the text. (*Cf.* Fig. 110.)

to early Palaeozoic times; the same is true of our modern cycads, maidenhair tree (Ginkgo), club-mosses (Lycopodiales), and horse-tails (Equisetales). The Coniferales may be traced back into the upper Carboniferous period, while the most highly developed of modern plants, the Angiosperms, appear to have come into existence as late as about the middle of the Mesozoic era, perchance as

TABLE V

Ascendancy	Periods	Persistence and relationship of great groups
VII. Reign of Angiosperms	Tertiary Cretaceous Comanchian	Ginkgoales, Coniferales, Gnetales, Monocotyls, Dicotyls, Cycadeoids, Cycads, Cycadofilicales, Sphenophyllales, Equisetales, Lycopodiales, Araucariales, Filicales
VI. Reign of Pro-angiosperms	Jurassic Triassic Permian	
V. Reign of Acrogens (Higher Equisetes. Lycopods, etc.)	Pennsylvanian Mississippian	Cordaitales
IV. Reign of Gymnosperms	Devonian	
III. Reign of Early Land Plants	Silurian Ordovician	5. Actual Fossil Land Plant record begins 4. Primofilices—Early Equisetes 3. Basal Plant Complex with variety of species
II. Reign of Algæ	Cambrian Precambrian (Proterozoic)	2. Differentiation of Dry Land and Aquatic Plants (Fossil Algæ abundant)
I. Reign of Primitive Life (Hypothetical)	Old Precambrian (Archeozoic)	(Fossil Algæ begin) 1. Primitive Protoplasm and Unicellular Life

In the above table (after Wieland), the groups are to be considered as arranged on an unrolled cylinder, projected from a hemisphere; thus the phyletic lines are to be pictured as converging below toward the pole, and the Cordaitales as coming between the Ginkgoales and Filicales, to both of which they are related.

recently as 20 million years ago. The lateness of their appearance and the rapidity with which they have spread, until they are now the dominant element in the flora of the land, indicate how well they are adapted to their environment. "Nothing is more extraordinary in the history of the vegetable kingdom," wrote Darwin to Hooker, "than the *apparently* very sudden or abrupt development of the higher plants."

"The construction of a pedigree of the Vegetable Kingdom is a pious desire, which will certainly not be realized in our time; all we can hope to do is to make some very small contributions to the work. Yet we may at least gather up some fragments from past chapters in the history of plants, and extend our view beyond the narrow limits of the present epoch, for the flora now living is after all nothing but one particular stage in the evolution of the Vegetable Kingdom."[1]

154. The Element of Geological Time.—How many years has it taken for the evolution of the higher Angiosperms—that is, from the dawn of the fossil record in the Silurian period to the present? No one knows. From a study of the thickness of rock strata, and a knowledge of the probable time required for the depositing of those strata as sediment on the floor of the ancient oceans, and their elevation and denudation to their present condition by weathering and erosion, geologists have been able to suggest relative measures of geologic time. Paleozoic time is *long*, twice as long as Mesozoic time, and Mesozoic time must be at least twice as long as Cenozoic time. The actual age of the earth is, however, a problem which engages the attention of physicists as well as geologists.

[1] Scott, D. H. "Studies in Fossil Botany," p. 3.

Sixty years ago Lord Kelvin gave a mean estimate of 100,000,000 years. With this estimate two geologists, Walcott and Geikie, have nearly concurred; but since the discovery of radium it has been estimated that certain carboniferous iron ores have an age of 140,000,000 years.

Figures of such magnitude convey but little meaning to our minds; they are too large for us to grasp their real value. "Therefore," as Darwin has said, "a man should examine for himself the great piles of superimposed strata, and watch the rivulets bringing down mud, and the waves wearing away the sea-cliffs, in order to comprehend something about the duration of past time, the monuments of which we see all around us."

CHAPTER XIII

THE GREAT GROUPS OF PLANTS

155. The entire question of taxonomic groups is very difficult and intricate, and there is at present a considerable difference in opinion and usage, even among those equally competent to judge. As set forth in Chapter IX, the segregation and sequence of larger groups may be based chiefly upon the morphology of living plants, or upon that basis supplemented by the findings of anatomy (including embryology and histology), comparative life histories, and paleobotany.[1] Manuals and "Floras" of systematic botany are, for the most part, arranged upon the former basis, which operates at present in the direction of conservatism and few changes in connection with the largest groups, or phyla. Regard for the evidence from other sources is more apt to result in conflict of opinion and more frequent revisions in the light of new studies, but it is also more apt to result in a closer approximation to the truth. In the former case the sequence of groups is chiefly based upon complexity of organization, proceeding from the simpler to the more complex. On this basis the monocotyledons, for example, would precede the dicotyledons, the order observed in the Manuals.

In the latter case the sequence of groups attempts to indicate or reflect their order of development in time, as indicated by the data of paleobotany, comparative life-histories, comparative anatomy, and plant geography. On this basis the monocotyledons would follow the

[1] See, also, p. 236.

dicotyledons, as being derived from the latter by a process of simplification (*Cf.* p. 223). The structural and anatomical evidence that eusporangiate ferns are more ancient than leptosporangiate ferns is rendered more certain by the fact that the earliest fern fossils (in Paleozoic rocks) are eusporangiate; the leptosporangiate forms do not appear until later, and the fossils belong to families closely related to the more ancient eusporangiate group, while the fossils of more recent rocks show closer affinities with the modern living forms. (See, however, p. 30.)

In any tabular arrangement including all the great groups or phyla every group must, of course, come definitely after some one group and precede another. Thus, mosses logically fall between the Thallophytes and the fern allies; but there is scarcely any evidence that they are phylogenetically related to the groups that follow them in the table. Strangely enough, there are few well-authenticated fossil remains of mosses (and those not below the Mesozoic), and it has even been seriously suggested that they may have developed from more complex groups by processes of reduction and simplifications; but there is little, if any, evidence to indicate from what higher group they might have been thus derived, and the positive, though meager, fossil evidence is sufficient to render highly improbable, if not to nullify, the suggestion of derivation by reduction.

The old group "Pteridophytes," of the manuals, including the true ferns and their "allies" (horsetails, lycopods, and little club-mosses), served a useful purpose before the recent researches in fossil botany; but the results of those studies have made it impossible consistently to maintain the group longer in its former con-

notation. The term "Pteridophyta" may still be used to advantage in a more restricted sense, as applying to the "true ferns," while the "fern allies" naturally fall into two other Divisions or phyla, namely the Club-mosses (*Lepidophyta*) and the Horsetails (*Calamophyta* of Bessey, or *Arthrophyta* of Berry).

The discovery of the fossil seed-bearing ferns (Cycadofilicales) and their fossil and living relatives (Hemicycadales, Cycadales, Cordaitales, and Ginkgoales), all having cryptogamic (*i.e.*, centripetal) wood,[1] and all the living forms distinguished from the other gymnosperms by the possession of ciliated motile sperms, suggested the group to which Jeffrey has given the convenient and descriptive term *Archigymnospermæ* (Early Gymnosperms): in contrast to the Yews (Taxales), Conifers (Pines, Spruces, Hemlocks, Firs, Cypress, etc.), and Gnetales, which lack both those characters. To this latter group Jeffrey has given the name, *Metagymnospermæ* (Late Gymnosperms).

Other authors have suggested grouping the woody-stemmed and comparatively small leaved Cordaitales, Ginkgoales, and Coniferales together, and apart from

[1] The first formed woody tissue is primary wood or *protoxylem*. It is present when the organ (stem, root, etc.) is young, and its cell walls are thickened in rings or spirals and thus it can readily stretch as the organ elongates in growth. After growth in length has ceased, or has been greatly retarded, secondary wood or *metaxylem*, forms. The cell walls of this tissue have scalariform, reticulate, or pitted thickening, and thus they cannot readily stretch. In the vascular cryptogams (*e.g.*, Club-mosses and related forms) the secondary wood forms inside the zone of primary wood; in the later or "higher" gymnosperms (Metagymnosperms) this order of development is reversed; while in the ferns and lower gymnosperms (*Archigymnosperms*) the earlier development is centripetal and the later centrifugal. Thus the mode of development of the woody tissue is an index of the evolutionary position of a given form.

the Cycadean series (Cycadales, Hemicycadales (Bennettitales), Cycadofilicales) which have pithy stems; but some of the Cordaitean forms also have pithy stems and comparatively large leaves. Here again, as so often, an attempt at a formal classification necessitates drawing an apparently sharp line where in fact one does not exist. As Professor Jeffrey[1] has said, the term Archigymnospermæ is one of convenience, and like most scientific terms falls short of covering the situation. On the basis of certain criteria (*e.g.*, the structure of the wood), the Ginkgoales appear to be intermediate between the Coniferales and the Cordaitales. In fact, as Jeffrey[2] has pointed out, the "living fossil," *Ginkgo*, may be regarded as a connecting link or transitional form between the Archigymnospermæ and the Metagymnospermæ.

The relationship of *Isoetes* is one of the most difficult to determine among all the vascular cryptogams. Arguments for and against interpreting it as derived by reduction from the *Lepidodendron* group are given by Lady Isabel Browne.[3] The secondary growth in thickness of its stem (in such a dwarfed form) must be regarded as a character of long standing, not recently acquired; plants in both groups have mucilage cavities. *Isoetes* resembles some of the Lepidodendrales (*e.g.*, the so-called *Stigmaria*[4]) in the dichotomous branching of its roots. Other facts of structure (*e.g.*, the occurrence of the sporangia on the upper side of the leaves) have also been interpreted

[1] Jeffrey, E. C *Science*, N. S. **47**: 316. 1918.

[2] Jeffrey, E. C. *The anatomy of woody plants*, p. 315. Chicago, 1917.

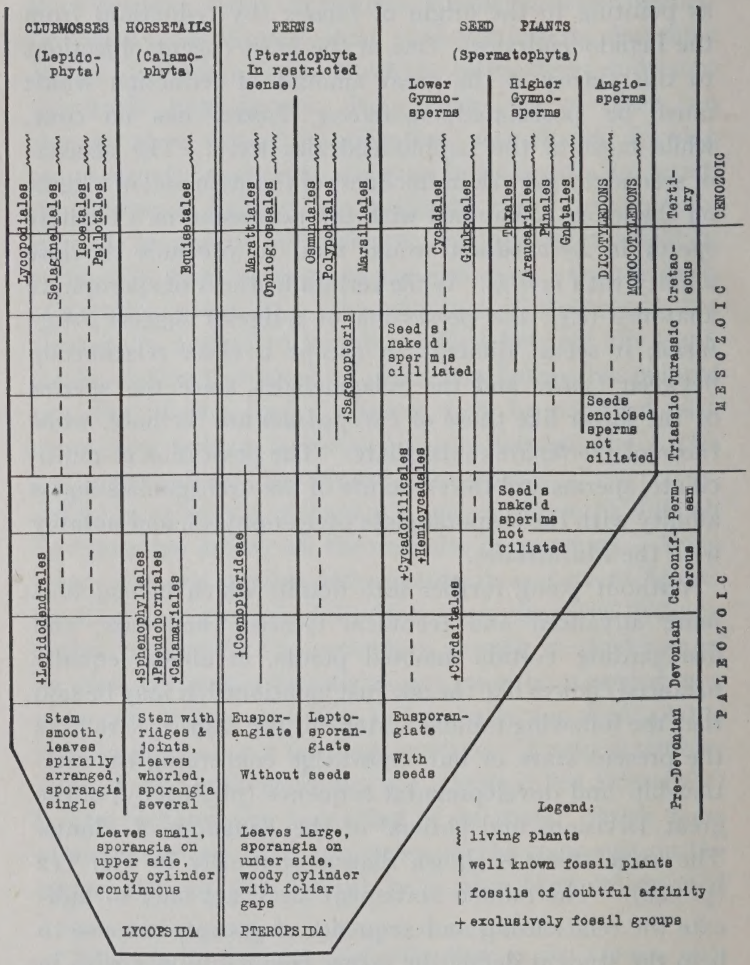
[3] Browne, Lady Isabel. The phylogeny and inter-relationships of the Pteridophyta. *New Phytologist* **7**: 93, 103, 150, 181, 230. 1908.

[4] The fossil remains to which the generic name *Stigmaria* was assigned have long been known to be the root-system of *Sigillaria*.

as pointing to the origin of *Isoetes* (by reduction) from the Lepidodendrales. One of the most cogent objections to this theory is the great amount of reduction which must be postulated; moreover, *Isoetes* has no cone, while most of the Lepidodendrales have. The absence of secondary growth in thickness of the stem and of a ligule on the leaves, combined with the possession of a biciliate sperm, in *Lycopodium*, would tend to preclude its close affinity with *Isoetes*. While certain features of sporophyte anatomy (*e.g.*, the possession of a ligule) suggest *Selaginella*, it seems difficult to accept a close relationship between *Isoetes* and the Selaginellales, since the sperms of the latter like those of *Lycopodium* are biciliate, while those of *Isoetes* are multiciliate. The possession of multiciliate, sperms and the structure of the archegonia suggest affinity with the eusporangiate pteridophytes, and notably with the Marattiales.

Without going further into details which belong to a more advanced and technical treatise than this, and disregarding certain mooted points, or almost equally balanced choices like the one just mentioned, it may be said that the following tabular statement (pp. 249–251) reflects the present state of our knowledge concerning the relationship and developmental sequence (phylogeny) of the great Divisions and Orders[1] of the Kingdom of Plants. The same thing is shown diagrammatically in Fig. 112 (p. 248). The tabular statement aims, not only to indicate the relationship and sequence of groups, but also to help the student define the terms commonly met with in the established literature of botany.

[1] Attention is called, in passing, to the uniform termination (-ales) of the plant Orders.



MAIN GROUPS OF VASCULAR PLANTS

Their apparent affinities and approximate geological distribution

FIG. 112.

TABLE VI

THE GREAT GROUPS OF THE KINGDOM OF PLANTS

MAIN GROUPS OF NON-VASCULAR PLANTS

Plants without "flowers"—CRYPTOGAMS (Nos. 1–5)
Plant body usually a thallus; sexual organs usually one celled.....**Thallophytes** 1
No archegonia
Chlorophyll-bearing.....*Algæ* 1*a*
Non-chlorophyll bearing.....*Fungi* 1*b*
Plant body thalloid or leafy; sexual organs usually several celled.....**Bryophytes** 2
Archegonia
Protonema rudimentary or wanting, sporophytes with elaters.....*Liverworts* 2*a*
Protonema well defined, sporophytes without elaters.....*Mosses* 2*b*

1. **Thallophytes**

1a. Algæ

Cyanophyceæ (Blue-green)
Chlorophyceæ (Green)
Phæophyceæ (Brown)
Rhodophyceæ (Red)

1b. Fungi

Myxomycetes (Slime-molds)
Schizomycetes (Bacteria)
Phycomycetes (Molds)
Ascomycetes (Spores in sacs)
Including most *Lichens* (*Ascolichenes*)
Basidiomycetes (Spores on stalks)
Including the *Basidiolichenes*
Fungi imperfecti (Life histories imperfectly known).

2–6*b*, *Archegoniates*; 2–6*c*, *Embryophyta*

2. **Bryophytes**

2a. Liverworts

Ricciales
Marchantiales
Jungermanniales
Anthocerotales

2b. Mosses

Spagnales (Peat mosses)
Andreæales (Black mosses)
Bryales (True mosses)

MAIN GROUPS OF VASCULAR PLANTS

Woody cylinder continuous, (*i.e.*, without foliar gaps), leaves small, sporangia above—LYCOPSIDA

3–5, *Vascular Cryptogams*

Stem smooth, leaves spirally arranged, sporangia single. **Clubmosses** 3
Stem with ridges and joints, leaves whorled, sporangia several. . . . . **Horsetails** 4
Woody cylinder discontinuous (*i.e.*, with foliar gaps), leaves large, sporangia below—PTEROPSIDA
Without seeds. . . . . **Ferns** 5
With seeds—SPERMATOPHYTA (PHANEROGAMS) . . . . . **Seed Plants** 6
Ovules naked, endosperm formed before fertilization. *Gymnosperms* 6
Sperms ciliated. . . . . *Early Gymnosperms* 6*a*
Sperms not ciliated. . . . . *Late Gymnosperms* 6*b*
Ovules enclosed, endosperm formed after fertilization . *Angiosperms* 6*c*

3. **Clubmosses** (*Lepidophyta* (Bessey))

Lycopodiales	Selaginellales
Isoetales (?)	Lepidodendrales (*Fossil*)
Psilotales	

4. **Horsetails** (*Calamophyta* (Bessey), *Sphenopsida* (Scott), *Arthrophyta* (Berry))

Spenophyllales (*Fossil*)	Calamariales (*Fossil*)
Pseudoborniales (*Fossil*)	Equisetales

5. **Ferns** (*Pteridophyta*, in restricted sense; *Filicineæ*).

Eusporangiatæ	*Leptosporangiatæ*
Primofilices (Cœnopterideæ)	Osmundales
Marattiales	Polypodiales
Ophioglossales	Marsiliales
(Isoetales?)	

6. **Seed-Plants**

(6*a* & 6*b* *Gymnospermæ* of Brongniart)

6*a*. *Early Gymnosperms* (*Cycadophyta* (Nathorst) except Ginkgoales; *Archigymnospermæ* (Jeffrey))

Cycadofilicales (*Fossil*)	Cordaitales (Fossil)
Hemicycadales (Wieland) = Bennettitales of Potonié (*Fossil*)	Ginkgoales
Cycadales	

6*b*. *Late Gymnosperms* (Coniferæ (Hallier); Metagymnospermæ (Jeffrey); *Strobilophyta* (Bessey))

Taxales	Pinales
Araucariales	Gnetales

6c. *Angiosperms* (Angiospermæ; Anthophyta (Braun))

Two cotyledons, leaves net-veined, parts of the flower in 5's or 4's —DICOTYLEDONS

Apetalæ (petals wanting)

1. Casuarinales
2. Piperales
3. Salicales
4. Myricales
5. Leitneriales
6. Balanopsidales
7. Juglandales
8. Fagales
9. Urticales
10. Proteales
11. Santalales
12. Aristolochiales
13. Polygonales
14. Chenopodiales

Polypetalæ (petals distinct—wanting in a few exceptional cases)

1. Ranales
2. Papaverales
3. Sarraceniales
4. Rosales
5. Geraniales
6. Sapindales
7. Rhamnales
8. Malvales
9. Parietales
10. Opuntiales
11. Thymeliales
12. Myrtales
13. Umbellales

Sympetalæ; Gamopetalæ (petals more or less united)

1. Ericales
2. Primulales
3. Ebenales
4. Gentianales
5. Polemoniales
6. Plantaginales
7. Rubiales
8. Valerianales
9. Campanulales

One cotyledon, leaves usually parallel-veined, parts of the flower in 3's or 6's—MONOCOTYLEDONS

1. Naiadales
2. Pandanales
3. Graminales
4. Palmales (Principes)
5. Cyclanthales (Synanthæ)
6. Arales
7. Xyridales
8. Liliales
9. Scitaminales
10. Orchidales

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